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**“Diving in the Verde Island Passage, Philippines”**  
(See Van Syoc, R., et al., Host Specificity in Sponge-inhabiting Barnacles, p. 329)  
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## **Taxonomic and Nomenclatural Notes on Six Genera of Acanthaceae in the West Indies**

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**The West Indies contains about 10,000 species of seed plants and 115 species of Acanthaceae. Taxonomic and nomenclatural notes are provided for the following six genera of West Indian Acanthaceae: *Barleriola*, *Dasytropis*, *Salpicantha* (= *Neriacanthus* s.s.), *Samuelssonina*, *Sapphoa*, and *Stenandrium*. Lectotypes are designated for *Barleriola inermis*, *B. multiflora*, *B. reedii*, *B. solanifolia*, *Dasytropis fragilis*, *Salpicantha purdieana*, *Samuelssonina verrucosa*, *Stenandrium crenatum*, *S. ekmanii*, *S. glabrescens*, *S. ovatum*, *S. undulatum*, *S. tuberosum*, and *S. wrightii*. A type is designated for *Stenandrium* sect. *Sphaerostenandrium*.**

The West Indies contains about 10,000 species of seed plants (spermatophytes), with as much as 70% of the flora being endemic to these islands (Acevedo-Rodríguez and Strong 2012). An estimated 21 genera and 115 species of Acanthaceae are native to the West Indies (Acevedo-Rodríguez and Strong 2012). Modern taxonomic revisions are lacking for many genera of Acanthaceae that occur there. The purpose of this treatment is to synthesize taxonomic and nomenclatorial information concerning six genera of Acanthaceae, representing three tribes of subfamily Acanthoideae, native to the West Indies.

Five of the genera treated here are endemic to the West Indies: *Barleriola* Oerst., *Dasytropis* Urb., *Salpicantha* Hook. (= *Neriacanthus* Benth. s.s.), *Samuelssonina* Urb. & Ekman, and *Sapphoa* Urb. The genus *Stenandrium* Nees, which is possibly restricted to the New World (McDade et al. 2005, 2008), is also included. Molecular phylogenies have indicated a close relationship between *Salpicantha*, *Stenandrium*, and *Holographis* Nees (McDade et al. 2005). Relationships among the other genera remain poorly understood.

Three species considered here are endemic to Haiti (*Barleriola multiflora* Urb. & Ekman, *Samuelssonina verrucosa* Urb. & Ekman, and *Stenandrium undulatum* Urb. & Ekman). These three species are of significant conservation concern, because we are unaware of any collections subsequent to their respective type collections, which were all made about 100 years ago. Recent floristic surveys in Haiti did not report additional occurrences for these three species (Judd 1987; Peguero et al. 2006). Additionally, *Samuelssonina*, as currently treated, is a monospecific genus.

Synonymy largely follows previous treatments. Many of the taxa within *Sapphoa* and *Stenandrium* from the West Indies are in need of further study to clarify taxonomic circumscriptions and distinctions.

Several type specimens are located and 14 lectotypifications are designated here, following the recommendations of McNeill (2014). Some type specimens were located through the collector information given by Stafleu et al. (1976–2009). To determine the authorship of the annotations on

specimens, handwriting samples were consulted through references given in Stafleu et al. (1976–2009) and samples provided by Burdet (2013) and Smith (1957). Specimens (other than types) used in this study are listed in an Appendix. Specimens that were seen in person are denoted with an exclamation mark. Herbarium acronyms follow Thiers (2015).

#### TYPIIFICATION OF NAMES BY LINNAEUS, SWARTZ, GRISEBACH, AND URBAN

We are unaware of any lectotype designation for *Barleria solanifolia* L. (= *Barleriola solanifolia* (L.) Oerst. ex Lindau) or *Gerardia tuberosa* L. (= *Stenandrium tuberosum* (L.) Urb.) (Jarvis 2007). In the protologues of these species, Linnaeus (1753) cited descriptions and plates of Plumier (1703) that portray flowers and fruits but not vegetative details. The plate of *Barleria* in Plumier (1703) apparently only depicts *Ruellia coccinea* (L.) Vahl (= *B. coccinea* L.; Burman 1756). The plates of Plumier reproduced in Burman (1756) include vegetative characters, and their accompanying Latin descriptions closely match those of the Linnaean protologues of *Barleria solanifolia* and *Gerardia tuberosa*. Linnaeus (1763: 848, 887) later cited the plates of Plumier that were reproduced in Burman (1756). These plates are presumed to have been available to Linnaeus before publishing his descriptions of *B. solanifolia* and *G. tuberosa* in 1753 (Polhill and Stearn 1976; Jarvis 2007) and are here designated the lectotypes. Linnaeus is not known to have seen any herbarium material of these species for his descriptions (see Pennell 1930; DeWolf 1957; Turland and Jarvis 1997).

Swartz published the names *Ruellia rupestris* Sw. and *R. scabrosa* Sw., and their respective holotypes are considered to be the specimens with the handwritten note “Herb. Swartzii” at S.

Three names considered here, *Anthacanthus bispinosus* Griseb., *Barleria saturejoides* Griseb., and *Stenandrium punctatum* Griseb., were coined by Grisebach from collections of Charles Wright. The type specimens of these names in Grisebach’s herbarium residing at GOET are recognized as the holotypes.

Urban described many species in the West Indies (some co-authored with Ekman), often from specimens collected by Ekman (Nordenstam et al. 1994). Of the species of Acanthaceae studied here, no type specimens could be located at B where Urban had worked; if any type specimens were held at B they were likely destroyed during World War II (Hiepko 1987). Howard (1952:84) noted that “Ekman’s specimens were sent to Urban for study and the majority of the types are now in the Riksmuseum in Stockholm. Unfortunately many of the types were kept in Berlin and were destroyed during the war.” Apparently, a complete or nearly complete set of Ekman’s types of Acanthaceae is extant at S. Those that bear Urban’s handwriting were presumably used by him in formulating protologues, and subsequently returned to S. A type specimen at S is here designated as the lectotype if it bears Urban’s handwriting (unless it is the only known specimen and is thus regarded as a holotype). Any duplicates at S that lack his annotation are treated as isolectotypes. Samples of Urban’s handwriting match the handwritten taxonomic names, authors, and others words (e.g. “typus,” “gen. nov.” or “spec. nov.”) on the labels of the lectotypes designated here. Additional details concerning the location, date, or plant description on the type specimens of species in *Barleriola*, *Dasytropis*, *Samuelssonia*, and *Sapphoa* do not always match Urban’s handwriting. However, on four lectotypes of species of *Stenandrium*, Urban apparently did write in most of these additional details.

## TAXONOMIC TREATMENT

**BARLERIOLA** Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854:136. 1855.

**TYPE.**— *Barleriola solanifolia* (L.) Oerst. Figure 1.

**DISCUSSION.**— The current concept of *Barleriola* (Barlerieae) recognizes four species of shrubs native to Cuba, Hispaniola, and Puerto Rico (Acevedo-Rodríguez and Strong 2012). Liogier (1995) distinguished *Barleriola* from the nearly exclusively Old World *Barleria* L. by its five-lobed (vs. four-lobed) calyx, two-seeded (vs. four-seeded) capsule, and smaller (vs. larger) flowers.

Key to the species of *Barleriola*

- 1a. Leaves prominently lobed . . . . . 2  
 1b. Leaves entire to crenate to weakly dentate . . . . . 3  
 2a. Inflorescence to 1.5 cm long, bracts short-acuminate at the apex . . . . . 1. *B. inermis*  
 2b. Inflorescence (1–) 1.5–12 cm long, bracts gradually tapering towards apex . . . 2. *B. multiflora*  
 3a. Axillary spines absent . . . . . 3. *B. saturejoides*  
 3b. Axillary spines present, to 1.8 cm long . . . . . 4. *B. solanifolia*

**1. *Barleriola inermis*** Urb. & Ekman, Ark. Bot. 22A(8):90. 1928. **TYPE.**— DOMINICAN REPUBLIC. **Azua:** Cordillera Central, Loma Nalga de Maco, headwaters of Arroyo del Valle, in forest, ca. 1350 m, 8 Jun 1926, *Ekman H-6282* (lectotype, designated here: S [no. R-7683]; isolectotypes: K!, NY, S [09-8549], US). Figure 1A.

**DISCUSSION.**— *Barleriola inermis* is endemic to the Dominican Republic.

**2. *Barleriola multiflora*** Urb. & Ekman, Ark. Bot. 22A(8):91. 1928. **TYPE.**— HAITI. **Ouest:** Massif de la Salle, Port-au-Prince, near Chapelle Malanga, ca. 1100 m, steep rocky slope, 27 Jan 1926, *Ekman H-5459* (lectotype, designated here: S [09-8556]; isolectotypes: F, G, GH, K!, NY, S [S-R-7684], US). Figure 1B.

**DISCUSSION.**— *Barleriola multiflora* is endemic to Haiti.

**3. *Barleriola saturejoides*** (Griseb.) M. Gómez, Anales. Soc. Esp. Hist. Nat. 23: 281. 1894. *Barleria saturejoides* Griseb., Cat. Pl. Cub. 195. 1866. **TYPE.**— CUBA. **Province unknown:** Potrero San Andrés, *Wright 3059* (holotype: GOET; possible isotypes: GH, K!, P, S, US).

*Barleriola reedii* Ekman ex Urb., Repert. Spec. Nov. Regni Veg. 20:309. 1924. **TYPE.**— CUBA. **Camagüey:** Pastelillo, near Nuevitas, on loose limestone rocks, 8 Oct 1922, *Ekman 15430* (lectotype, designated here: S [05-306]; isolectotypes: GH, NY, K!, UC!, US). Figure 1C.

**DISCUSSION.**— *Barleriola saturejoides* is endemic to Cuba (Acevedo-Rodríguez and Strong 2012). *Barleriola reedii* was listed as a synonym by León and Alain (1957). Borhidi and Muñiz (1972) recognized three subspecies based on pubescence. These subspecies appear to intergrade. The type locality of *B. saturejoides* is based on Howard (1988), who was unable to determine the geographic location of this place. There is a Potrero San Andrés about 6 km NW of Jicotea in the province of Villa Clara, but it is not certain that this is the same Potrero San Andrés at which Wright collected.

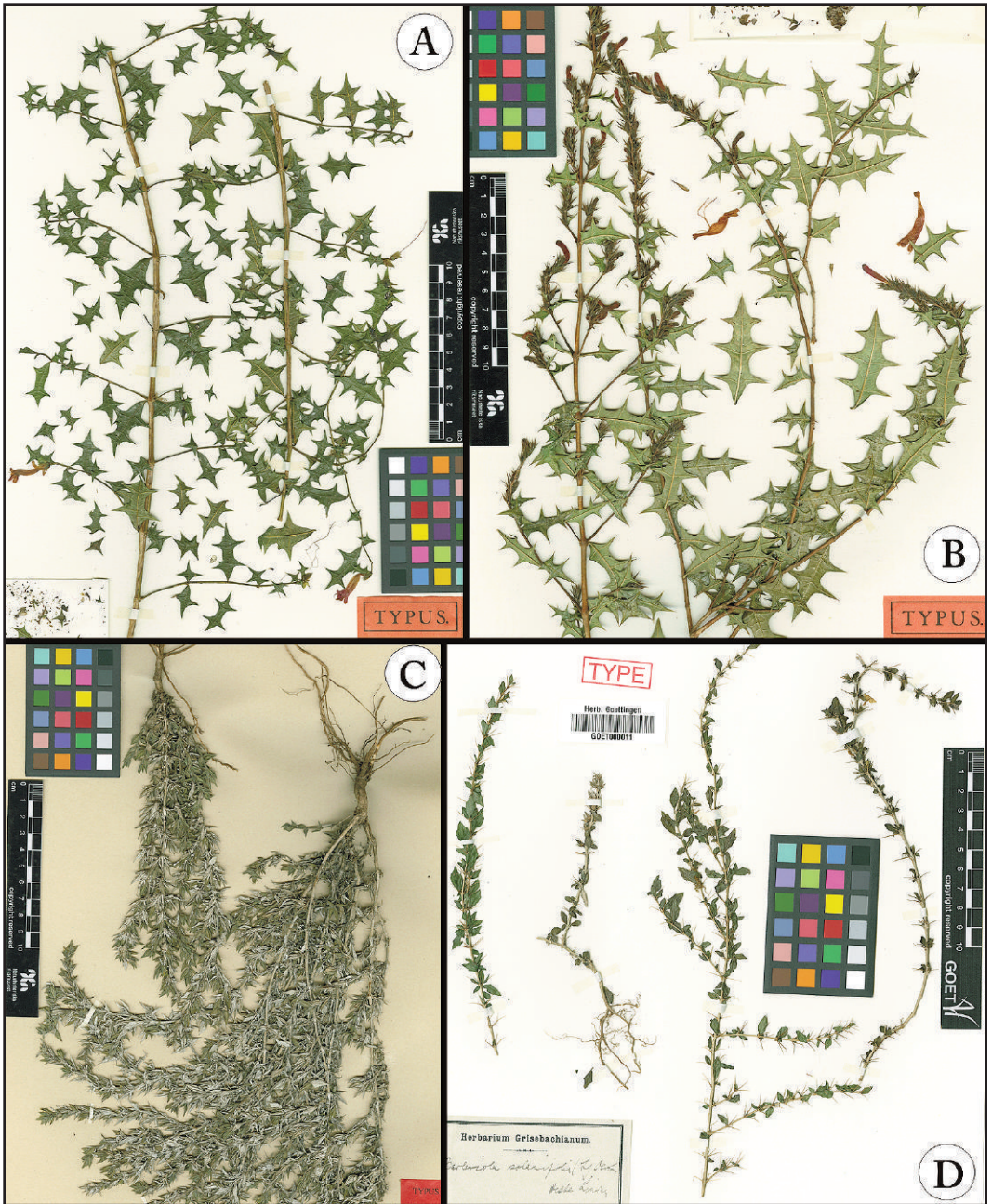


FIGURE 1. A. Lectotype of *Barleriola inermis*, Ekman H-6282 [R-7683]. B. Lectotype of *Barleriola multiflora*, Ekman H-5459 [09-8556]. C. Lectotype of *Barleriola reedii* (= *B. saturejoides*), Ekman 15430 [05-306]. D. Holotype of *Anthacanthus bispinosus* (= *Barleriola solanifolia*), Wright 1342 [000011].

**Key to the subspecies of *Barleriola saturejoides***

- 1a. Stems and leaves glabrate . . . . . 3a. subsp. *satuejoides*  
 1b. Stems and leaves pubescent . . . . . 2  
 2a. Stems and leaves short-pubescent . . . . . 3b. subsp. *acunae*  
 2b. Stems and leaves hirsute . . . . . 3c. subsp. *hirsuta*

**3a. *Barleriola saturejoides*** (Griseb.) M. Gómez subsp. *satuejoides*.

**3b. *Barleriola saturejoides*** (Griseb.) M. Gómez subsp. *acunae* Borhidi & O. Muñiz, Acta Bot. Acad. Sci. Hung. 17:28. 1972. **TYPE**.— CUBA. **Guantánamo**: S Baracoa, in fruticetis semideserticis inter Montecristo et Jauco, *Acuña 5193* (holotype: SV [incorporated into HAC]; isotype: ULV [fide Méndez Orozco 2008]).

**3c. *Barleriola saturejoides*** (Griseb.) M. Gómez subsp. *hirsuta* Borhidi & O. Muñiz, Acta Bot. Acad. Sci. Hung. 17:28. 1972. **TYPE**.— CUBA. **Santiago de Cuba**: In fruticetis siccis calcareis montis Loma el Palenque supra pag. Siboney, 23 Nov 1952, *López Figueiras 796* (holotype: LS [incorporated into HAC]; isotype: SV [incorporated into HAC]).

**4. *Barleriola solanifolia*** (L.) Oerst. ex Lindau, Bot. Jahrb. Syst. 18:63. 1893. *Barleria solanifolia* L., Sp. Pl. 2:636. 1753. *Barleriola solanifolia* (L.) Oerst. ex Lindau var. *humilis* M. Gómez, Anales Soc. Esp. Hist. Nat. 23:281. 1894, nom. illeg. **TYPE**.— Lectotype (designated here): Plumier's illustration in Burman, Pl. Amer., fas. 2, tab. 43, fig. 2. 1756.

*Aetheilema rigidum* Bartl., Index Seminum Hort. Acad. Gotting. 1. 1841. **TYPE**.— "Hab. in India occidentali" (specimen, if any exists, not located).

*Eranthemum cubensis* Spreng. ex Nees in Alph. de Candolle, Prodr. 11:726. 1847, nom. nud.

*Anthacanthus bispinosus* Griseb., Pl. Wright. 2:525. 1862. *Barleriola solanifolia* (L.) Oerst. ex Lindau var. *bispinosa* (Griseb.) M. Gómez, Anales Soc. Esp. Hist. Nat. 23:281. 1894. **TYPE**.— CUBA. **Guantánamo**: Prope villam Monte Verde dictam, Jan–Jul 1859, *Wright 1342* (holotype: GOET; possible isotypes: GH, K!, NY, P). Figure 1D.

*Barleriola solanifolia* (L.) Oerst. ex Lindau var. *lindeniana* M. Gómez, Anales Soc. Esp. Hist. Nat. 23:281. 1894, nom. nud.

**DISCUSSION**.— *Barleriola solanifolia* occurs in Cuba, Hispaniola, and Puerto Rico (Acevedo-Rodríguez and Strong 2012). Its pollen was depicted by Lindau (1893). Nees (1847: 243, 262) treated *Aetheilema rigidum* as a synonym. Gómez de la Maza (1894) proposed three varieties of *B. solanifolia*. His variety *humilis* is illegitimate because it included the basionym *Barleria solanifolia*. The variety *lindeniana* referenced the specimen *Linden 1830* (not seen by us) but provided no description or diagnosis. Gómez did not reference, directly or indirectly, Nees (1847:726) who used the same specimen to describe a variety without providing a name for it. The variety *bispinosa* was based upon *Anthacanthus bispinosus*, which was later treated as a synonym of *B. solanifolia* by Lindau (1900) and León and Alain (1957).

***DASYTROPIS*** Urb., Repert. Spec. Nov. Regni Veg. 20:310. 1924. **TYPE**.— *Dasytropis fragilis* Urb. Figure 2B.

**1. *Dasytropis fragilis*** Urb., Repert. Spec. Nov. Regni Veg. 20:311. 1924. **TYPE**.— CUBA. **Holguín**: Sierra de Nipe, Woodfred, in low forest on the slope towards Arroyo del Medio, 29 Sep 1922, *Ekman 15236* (lectotype, designated here: S [05-393]; isolectotypes: G, NY, US). Figure 2A.





**DISCUSSION.**— *Dasytropis* (Justicieae) is monospecific and occurs in the Sierra de Nipe region of eastern Cuba, an area possibly harboring the most endemics in the country (Carabia 1945). Vegetatively, this species greatly resembles *Sapphoa rigidifolia*. Both are found in eastern Cuba as scandent, vine-like shrubs (León and Alain 1957; Borhidi 1983). Additionally, material from both species is apparently delicate and fragile as their type specimens bear fragment packets with abundant material. Significant differences noted in their respective protologues consist of the presence of two staminodes and caerulean flowers in *Sapphoa*, and two stamens without staminodes and pale green-white flowers in *Dasytropis*.

**SALPIXANTHA** Hook., Bot. Mag. 71:tab. 4158. 1845. **TYPE.**— *Salpixantha coccinea* Hook.

*Neriacanthus* Benth. in Bentham and Hooker, Gen. Pl. 2:1096. 1876. **TYPE.**— *Neriacanthus purdieanus* Benth.

**DISCUSSION.**— *Salpixantha* (Acantheae) is endemic to Jamaica and contains two species. The two species are shrubs with spicate inflorescences and flowers containing four stamens (Adams 1972).

#### Key to the species of *Salpixantha*

- 1a. Corollas pinkish to red; inflorescence bracts to 2 mm long . . . . . 1. *S. coccinea*  
 1b. Corollas greenish white to white; inflorescence bracts 8–17 mm long . . . . . 2. *S. purdieana*

**1. *Salpixantha coccinea*** Hook., Bot. Mag. 71:tab. 4158. 1845. *Geissomeria coccinea* (Hook.) T. Anderson ex Griseb., Fl. Brit. W.I. 454. 1862. **TYPE.**— Lectotype, designated by Profice in 2002: Bot. Mag. 71: plate 4158. 1845. Figure 3A.

**DISCUSSION.**— *Salpixantha coccinea* is endemic to Jamaica. Purdie collected a specimen (*Purdie s.n.* at K ex hb. Hooker) of this species in November 1843 from “a small deep narrow gully near Great Valley, Manchester.” The label of this specimen notes that he also “found” the species “in the pedro District, St. Anns.” According to the same label, propagules of the species were sent to England by Purdie. In the protologue, Hooker (1845) indicated that plants were cultivated “in the stove” at the Royal Botanic Gardens, Kew, where they began flowering in 1844.

**2. *Salpixantha purdieana*** (Benth.) S. Moore, J. Bot. 65: 221. 1927. *Neriacanthus purdieanus* Benth. in Bentham and Hooker, Gen. Pl. 2:1096. 1876. **TYPE.**— JAMAICA. “Rocks nr Christiana, Manchester,” *Purdie s.n.* (lectotype, designated here: K! [K000534390]; isolectotypes: K! [K000534389], K! [K000569009], P [P00719541]); probable isolectotype: TCD!).

**DISCUSSION.**— *Salpixantha purdieana* is endemic to Jamaica. It has often been treated under *Neriacanthus*. Here it is included in *Salpixantha* because of the morphological (Lindau 1900; Moore 1927; Profice 2002; McDade et al. 2005) and molecular similarities (McDade et al. 2005) with *S. coccinea*, the type of *Salpixantha*. Several species in Central and South America have been included in *Neriacanthus* but do not appear to be congeneric with *S. purdieana* (McDade et al. 2005). Because *S. purdieana* is the type of *Neriacanthus*, these other Central and South American species of *Neriacanthus* may need to be accommodated under a different generic name or a different type for *Neriacanthus* could be conserved.

FIGURE 2 (left). A. Lectotype of *Dasytropis fragilis*, Ekman 15236 [05-393]. B. Illustration of *Dasytropis fragilis* from Urban (1924); 1. habit, 2. flower, 3. inside of flower, 4. stamen, 5. pollen, 6. gynoeceum, 7. capsule, 8. seeds, 9. part of leaf showing cystoliths, 10. pili; copyright Wiley-VCH Verlag GmbH & Co. KGaA; reproduced with permission. C. *Sapphoa rigidifolia*, Ekman 15975 [05-395]. D. Holotype of *Sapphoa rigidifolia*, Ekman 6794 [05-396].

Three specimens of William Purdie's plants of *Salpixinantha purdieana* are at K: 1) a specimen from Bentham's herbarium without flowers or specific locality data; it was possibly grown by Hooker at Kew (i.e., a note states: "Hooker 1844"); another note by William B. Hemsley states, "a small piece sent to Dr. I. Urban, Jan 1899," which indicates that a type fragment probably existed at B and was likely destroyed there; and it was annotated as "Type" by an unknown individual; 2) a specimen from W. J. Hooker's herbarium with locality data, a date (December 1843), and notes ("A beautiful shrub, 8 feet high" and "rare") that suggest a plant collected in the field; and 3) a robust specimen from Hooker's herbarium with flowers, locality information (apparently written in W. J. Hooker's hand) that concurs with that in the protologue (i.e., "rupibus provinciae Manchester Jamaicae;" Bentham 1876) and matches the location provided by J. D. Hooker (1876), and sketches of plant parts that are nearly identical to the illustrations in the plate published by J. D. Hooker (1876, Fig. 3B; this plate is also possibly original material as it was published in the same month, May, as the protologue). The latter specimen from W. J. Hooker's herbarium is chosen as the lectotype because of the greater amount of information on the sheet that conforms to the protologue.

*SAMUELSSONIA* Urb. & Ekman, Ark. Bot. 22A:96. 1928. Type.— *Samuelssonia verrucosa* Urb. & Ekman.

1. *Samuelssonia verrucosa* Urb. & Ekman, Ark. Bot. 22A(8):97. 1928. TYPE.— HAITI. **Nippes/Sud:** Massif de la Hotte, central group, St.-Louis-du-Sud, Bonnet-Carré, limestone, 1150 m, only one tree seen, 2 Nov 1927, *Ekman H-9232* (lectotype, designated here: S [05-397]; isolecotypes: CAS!, G, GH, K!, NY, S [05-398], US). Figures 3C, 3D.

**DISCUSSION.**— *Samuelssonia* (Justicieae) is monospecific and endemic to Haiti. Its one species was described as a 4–5 m tall tree with a 10 cm wide trunk and leaves with prominent, verrucose, semi-globose cystoliths. The inflorescence is axillary with flowers containing two stamens, but mature flowers and pollen are apparently unknown (Urban 1928). Urban (1928) remarked upon possible similarities with *Hoverdenia* Nees and *Justicia* L., but did not clarify how *Samuelssonia* differed. On the nearly 100-year-old type specimen, Ekman noted that only a single tree was encountered. The apparent lack of additional collections since then raises the possibility that it is extinct.

*SAPPHOA* Urb., Repert. Spec. Nov. Regni Veg. 18:24. 1922. Type.— *Sapphoa rigidifolia* Urb.

**DISCUSSION.**— *Sapphoa* (Justicieae) is endemic to serpentine soils of eastern Cuba and accumulates a moderate amount of nickel (Reeves et al. 1999). The two species are vine-like, scandent shrubs having flowers with two stamens and two staminodes (León and Alain 1957; Borhidi 1983).

#### Key to the species of *Sapphoa*

- 1a. Leaf cystoliths parallel to leaf veins; calyces 3–4 mm long. . . . . 1. *S. ekmanii*  
1b. Leaf cystoliths perpendicular to leaf veins; calyces 4–5 mm long. . . . . 2. *S. rigidifolia*

1. *Sapphoa ekmanii* Borhidi, Nordic J. Bot. 3:353. 1983. TYPE.— CUBA. **Guantánamo:** Sierra de la Iberia, Taco Bay, Baracoa, 11 Apr 1960, *López Figueiras U.O. 609* (holotype: HAC; isotypes: HAC, HAJB).

**DISCUSSION.**— *Sapphoa ekmanii* is tentatively recognized here but several of the characters

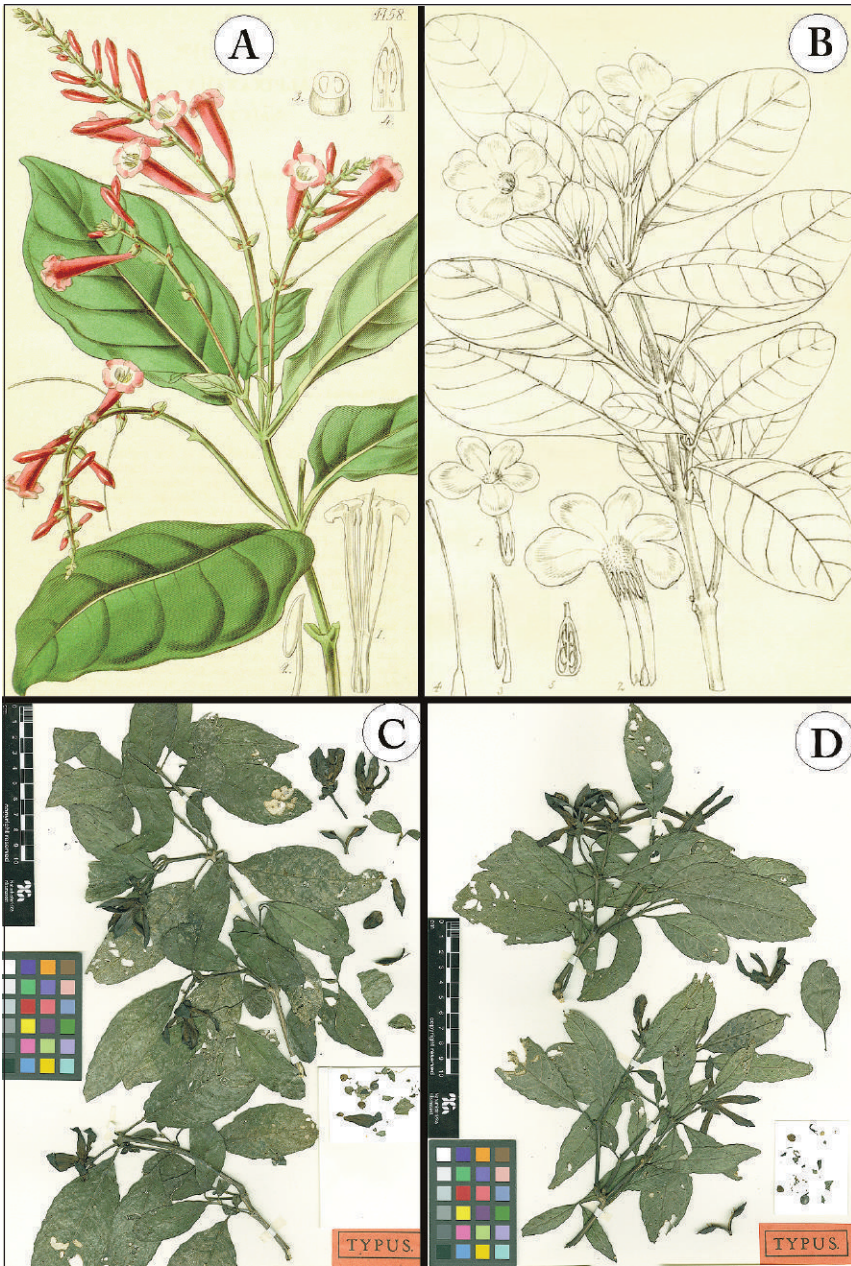


FIGURE 3. A. Lectotype of *Salpicantha coccinea* from Hooker (1845); 1. inside of flower, 2. stamen, 3. cross-section of ovary, 4. longitudinal section of ovary. B. Illustration of *Salpicantha purdieanus* from Hooker (1876); 1. flower, 2. inside of flower, 3. stamen, 4. gynoecium, 5. section of ovary. C. Isolectotype of *Samuelssonina verrucosa*, Ekman H-9232 [05-398]. D. Lectotype of *Samuelssonina verrucosa*, Ekman H-9232 [05-397].

used to differentiate it from *S. rigidifolia* seem tenuous. The distinguishing features of *S. ekmanii* (Borhidi 1983:353) were stated to be its "ovate, elliptic to lanceolate" leaves (vs. mostly obovate in *S. rigidifolia*), margins not revolute (vs. revolute), cystoliths lengthwise (vs. transverse), calyx 3–4 mm long (vs. 4–5 mm long), and corolla 1.3–1.7 cm long (vs. 2.2–2.5 cm). The holotype of *S. rigidifolia* contains ovate to elliptic leaves, a corolla about 1.8 cm long, and a calyx about 5 mm long. Thus, leaf shape and corolla length do not appear to be characters that support the recognition of two species. An additional specimen cited by Borhidi (1983) as *S. ekmanii* has slightly revolute leaves just as the holotype of *S. rigidifolia*. We only have seen images of the type specimens and have not examined the arrangement of the cystoliths to determine their utility in recognizing *S. ekmanii*. Cystoliths of West Indian *Barleriola* specimens at FTG are generally parallel to the leaf veins but can also be variably perpendicular within the same leaf, suggesting this may not be a good character to distinguish these species.

**2. *Sapphoa rigidifolia*** Urb., Repert. Spec. Nov. Regni Veg. 18:25. 1922. **TYPE.**— CUBA. **Holguín:** Sierra de Cristal, ad rivièrè in Lebisa affluent [Río Levisa], 650–1000 m, fructus scandens, flores caeruleus, 4 Mar 1916, *Ekman 6794* (holotype: S [05-396]). Figure 2D.

**STENANDRIUM** Nees, Nat. Syst. Bot. 444. 1836, nom. cons. **TYPE.**— *Stenandrium mandioccanum* Nees.

*Gerardia* L., Sp. Pl. 2:610. 1753, pro parte. **TYPE.**— *Gerardia tuberosa* L. Figure 4D.

**DISCUSSION.**— *Stenandrium* s.s. (Acantheae) contains ca. 50 species of perennial herbs and subshrubs distributed throughout the tropics and subtropics of the New World (Daniel 1984). Morphologically similar species from the Old World (= *Stenandriopsis* S. Moore) have been included in *Stenandrium* (e.g. Vollesen 1992), but molecular phylogenies (McDade et al. 2005) place the Old World *Stenandriopsis* apart from New World *Stenandrium*. Vollesen (1992), however, was unable to discern any discrete morphological differences between *Stenandriopsis* and *Stenandrium*.

A few infrageneric names within *Stenandrium* have been introduced, however, no comprehensive infrageneric classification of *Stenandrium* has been proposed. Therefore, the three infrageneric names will likely require additional studies to determine their taxonomic utility.

***Stenandrium* sect. *Stenandrium*.** *Stenandrium* Nees sect. *Schizostenandrium* Lindau, Nat. Pflanzenfam. 4(3b):321. 1895, nom. illeg. **TYPE.**— *Stenandrium mandioccanum* Nees.

**DISCUSSION.**— Two remarkably different pollen morphologies have been observed in *Stenandrium*: a prolate, tricolpate, aperturate type and a spherical, gemmate, inaperturate type. Lindau (1895) described two sections based on these two pollen types.

*Stenandrium* sect. *Stenandrium* is characterized by tricolpate pollen. Because Lindau included the type of *Stenandrium* (*S. mandioccanum*) in his sect. *Schizostenandrium*, his name for the section is superfluous for the autonym. Lindau (1893) provided an illustration of tricolpate pollen from *S. humboldtianum* Nees, which he included in this section. Lindau (1895) also included *S. rupestre* (Sw.) Nees (= *S. tuberosum* (L.) Urb.) from Hispaniola within this section.

***Stenandrium* sect. *Sphaerostenandrium*** Lindau, Nat. Pflanzenfam. 4(3b):321. 1895. **TYPE.**— *Stenandrium trinerve* Nees (designated here).

**DISCUSSION.**— *Stenandrium* sect. *Sphaerostenandrium* is characterized by gemmate pollen. Lindau (1895) included *S. dulce* (Cav.) Nees and *S. trinerve* in this section. Though *S. dulce* has

been reported to have the two different pollen types noted above, it is unclear which type of pollen the type material of *S. dulce* residing at MA possesses. This widespread species appears to have gemmate pollen in Argentina, Bolivia, Chile, Mexico, Paraguay, and Florida, U.S.A. (Lindau 1895; Ariza Espinar and Ferrucci 1982; Daniel 1998; Pire et al. 2003). However, some specimens from Brazil and Mexico assigned to this species have only tricolpate pollen (Lindau 1895; Daniel 1998). Because Ariza Espinar and Ferrucci (1982) reported that the original material of *S. trinerve* studied by Nees and residing at K has gemmate pollen, *S. trinerve* is here designated as the type of *S. sect. Sphaerostenandrium*. *Stenandrium trinerve* is now commonly treated as a synonym of *S. dulce* (Ariza Espinar and Ferrucci 1982; Ezcurra and Kameyama 2008). Lindau (1893) provided an illustration of gemmate pollen from *S. trinerve*. This section is not known from the West Indies.

### Key to 'Groups' of *Stenandrium* in the West Indies

- 1a. Leaves chartaceous, pilose, margin not revolute . . . . . "*S. tuberosum* complex"  
 1b. Leaves coriaceous, not pilose, margin revolute . . . . . *S. subg. Coriifolium*

### "*Stenandrium tuberosum* complex"

**DISCUSSION.**—The *Stenandrium tuberosum* complex comprises a variable group of small, acaulescent herbs. Because there is no comprehensive treatment of the West Indian taxa within the *S. tuberosum* complex, we feel unable to construct an adequate key based on the available literature and our review of limited specimens. Several authors have questioned the recognition of many taxa within this complex. The *S. tuberosum* complex requires further study to determine the number of taxa worthy of recognition, their ranks, and the characters that delimit them. Identification keys have been provided for Cuba (León and Alain 1957; Dietrich 1983) and the Bahamas (Correll and Correll 1982).

**1. *Stenandrium acuminatum*** Urb., Symb. Antill. 7:382. 1912. *Gerardia acuminata* (Urb.) S.F. Blake, Contr. Gray Herb. 52:100. 1917. **TYPE.**—HAITI. **Grand'Anse:** "Prope Corail ad occidentem versus in Plaine des Gommiers locis satis humidis umbrosis, 80 m. alt., m. Aug. flor. et fruct." (fide protologue), *Christ 2217* [not located].

**DISCUSSION.**—Moscoso (1943) and Liogier (1997) erroneously listed *Gerardia acuminata* as a synonym of *Barleriola solanifolia*.

In the protologue Urban (1912) indicated affinities between this species and *S. droseroides* from Cuba. The type of *S. acuminatum* has not been located. Eugène Christ's collections from Haiti (1899–1910) were deposited primarily at B (with duplicates at G, L, NY, US, and VEN) (Lanjouw and Stafleu 1954); additional specimens of his collections are at BR, GH, K, and M. The holotype was likely destroyed at B, and we have not located any duplicates to date. Liogier (1995) cited the type and five additional collections of the species from Haiti. One of these (Haiti: Massif de la Hotte, western group, between Maron and Maffrand, steep hillside, ca. 100 m, 5 Jul 1928, *Ekman 10276*, K!) was identified by Ekman (and confirmed by Urban's annotation) as this species. This plant pertains to the *S. tuberosum* complex and shows the following characteristics: rosulate perennial herbs to 1.5 dm tall from a woody rhizome; leaves chartaceous, long-petiolate (petiole mostly longer than blade), petioles 12–62 mm long, pubescent with flexuose eglandular trichomes to 1.5 mm long; blades elliptic, 21–50 x 12–25 mm, 1.8–2.3 x longer than wide, pubescent like petioles, rounded at apex, cuneate at base, surfaces punctate (less conspicuously so abaxially), margin sinuate, not revolute; spikes to 15 cm long, peduncle to 43 mm long, pubescent like petioles, fertile

portion of spike to 110 mm long, bracts lanceolate, 4.5–6 mm long, bracteoles lance-subulate, 2–2.3 mm long; calyces 2.5–3 mm long, corollas not seen; capsules 4 mm long, glabrous.

In his key to species of *Stenandrium* on Española, Liogier (1995) indicated that peduncles of this species were glabrous to glabrescent. Urban (1912) had described the peduncles as being “tenuiter pubescente,” which agrees with our observations of *Ekman 10276*. The glabrous capsules of *Ekman 10276* do not concur with descriptions of Urban (1912) and Ekman (1995) in which the capsules are described as distally pubescent with spreading trichomes.

**2. *Stenandrium arnoldii*** H. Dietr., *Wiss. Zeitschr. Friedrich-Schiller Univ. Jena, Math.-Naturwiss. Reihe* 33:725. 1984, non *S. arnoldii* (Mildbr.) Wassh. (1997), nom. illeg. **TYPE.**— CUBA. **Holguín:** Mpio. Mayarí, Pinares de Mayarí, camino entre Loma Estrella y Loma Gurugú, 700 m, 26 May 1983, *Bisse et al. Fl. de Cuba 50265* (holotype: HAJB; isotype: JE).

**DISCUSSION.**— *Stenandrium arnoldii* is endemic to Cuba. Dietrich (1984) distinguished *S. arnoldii* from “*S. droseroides* s. l.” and *S. tuberosum* by its smaller leaves (0.7–1.1 vs. 2–5 cm), smaller bracts (3.5–4 vs. 4–8 mm), and lack of (vs. presence) of tuberous roots.

**3. *Stenandrium bracteosum*** (Britton & Millsp.) Britton ex Leonard, *Wrightia* 2:77. 1960. *Gerardia bracteosa* Britton & Millsp., *Bahama Fl.* 402. 1920. **TYPE.**— BAHAMAS. **Mayaguana:** Abraham Bay and vicinity, in cultivated field, 6–8 Dec 1907, *Wilson 7472* (holotype: NY [00114975]; isotypes: K!, US). Figure 4E.

**DISCUSSION.**— *Stenandrium bracteosum* is endemic to the Bahamas. It was distinguished from *S. droseroides* by its stout peduncle (vs. delicately slender), longer bracts (8–12 vs. 3–7 mm), and pink (vs. white) corolla with a longer tube (7+ vs. 3–4 mm) (Correll and Correll 1982). The type specimen of *S. bracteosum* at NY is recognized as the holotype because the handwritten word “type” on its label resembles Britton’s handwriting. The specimen at US bears the note “fragment of type.”

**4. *Stenandrium carolinae*** Leonard & Proctor, *Wrightia* 2: 75. 1960. **TYPE.**— TURKS & CAICOS. **North Caicos:** Whitby, dry sandy soil, herb, flowers pink, 1 Jul 1954, *Proctor 9094* (holotype: US; isotype: A).

**DISCUSSION.**— *Stenandrium carolinae*, as currently recognized, is endemic to the Bahama Archipelago. Correll and Correll (1982) indicated it was possibly conspecific with *S. bracteosum* (e.g., both have large pustulate hairs) but separated the two based on a higher density of small curved hairs present on the upper surface of the leaves of *S. carolinae*.

**5. *Stenandrium crenatum*** Urb., *Symb. Antill.* 9:130. 1923. **TYPE.**— CUBA. **Santiago de Cuba:** Prope Aguadores, in scopulis siccis calcareis, 4 Nov 1917, *Ekman 8700* (lectotype, designated here: S [05-307]; isolectotype: NY). Figure 4G.

**DISCUSSION.**— *Stenandrium crenatum* is endemic to Cuba. The leaves of *S. crenatum* are crenate to undulate-crenate, whereas those of other species in the complex are said to be entire to occasionally repand (León and Alain 1957; Dietrich 1983).

**6. *Stenandrium droseroides*** Nees in Alph. de Candolle, *Prodr.* 11:284. 1847. *Gerardia droseroides* (Nees) S.F. Blake, *Rhodora* 20:68. 1918. **TYPE.**— CUBA. **Province unknown:** Wit-

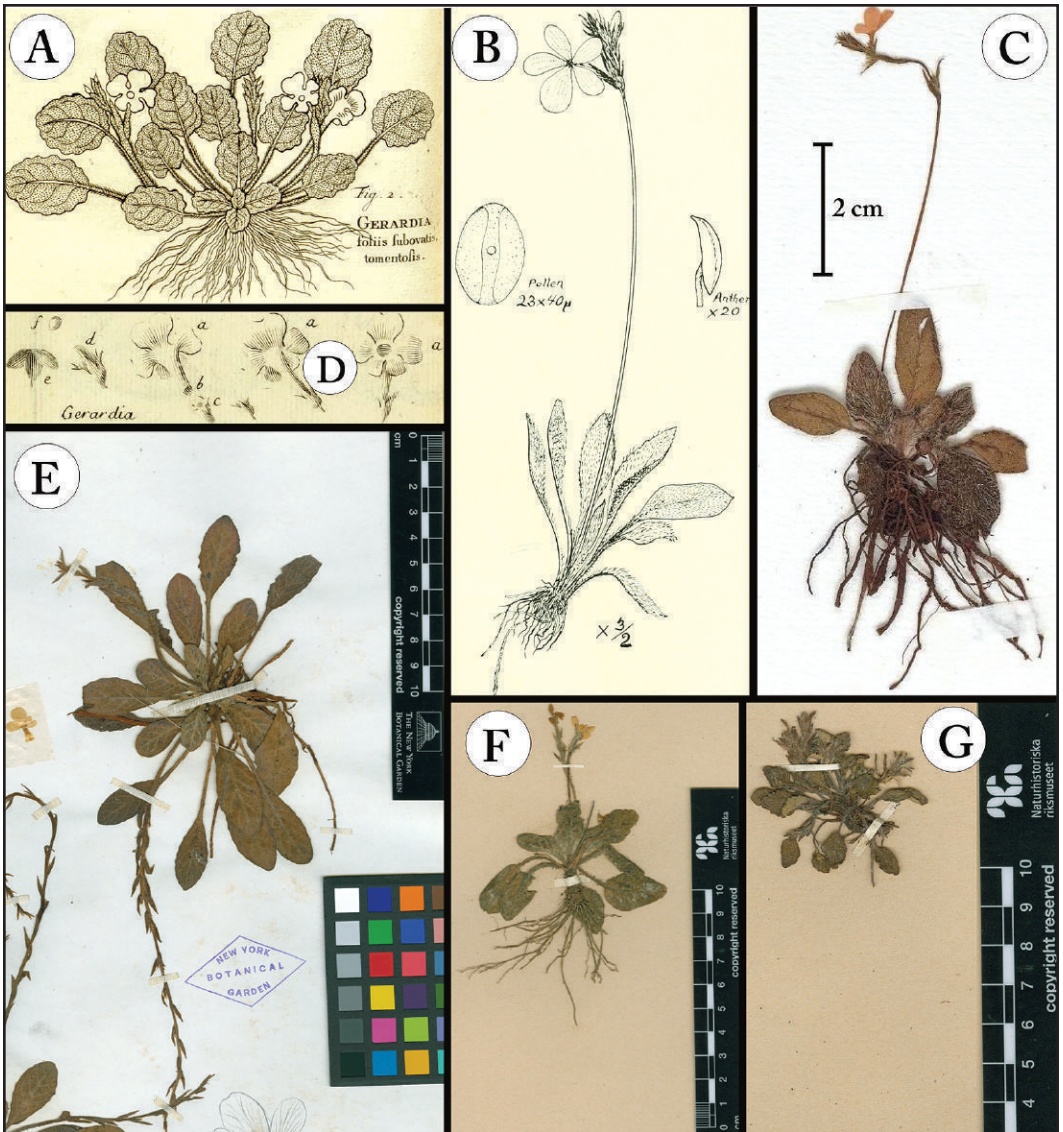


FIGURE 4. A. Lectotype of *Stenandrium tuberosum* from Burman (1756). B. Illustration of *Stenandrium pinetorum* from Jennings (1917). C. Isotype of *Stenandrium droseroides*, de la Sagra s.n. [000250674]. D. *Stenandrium* (likely *S. tuberosum*), part of tab. 12 with description from page 30 of Plumier (1703, as “*Gerardia*”); a. flower, b. corolla separated from c. calyx, d. capsule, e. septum, f. seed. E. Holotype of *Stenandrium bracteosum*, Wilson 7472 [00114975], courtesy of the C. V. Starr Virtual Herbarium of The New York Botanical Garden. F. Lectotype of *Stenandrium ovatum*, Ekman 10701 [05-310]. G. Lectotype of *Stenandrium crenatum*, Ekman 8700 [05-307].

hout locality, 1825, *de la Sagra s.n.* (holotype: G [00464094]; isotype: GZU [000250674]; probable isotype, P). Figure 4C.

**DISCUSSION.**— *Stenandrium droseroides* has been reported from the Bahamas (Britton and Millspaugh 1920; Correll and Correll 1982) and Cuba (León and Alain 1957; Dietrich 1983, 1984). Lindau (1900) noted minor differences between *S. droseroides* and *S. tuberosum* (as *S. rupestre*). He described bracts 6–7 mm long and pubescent foliage in *S. tuberosum* and bracts ca. 3 mm long and hirsute leaves in *S. droseroides*. León and Alain (1957) characterized bracts of *S. droseroides* as 3–5 mm long and Dietrich (1983) noted they were up to 9 mm long in *S. droseroides*. Dietrich (1984) then used the phrase “*Stenandrium droseroides* s.l.” but did not explicitly synonymize any names. Jennings (1917) expressed doubt that *S. acuminatum* and *S. droseroides* were distinguishable from *S. tuberosum*. The corollas of *S. droseroides* and *S. heterotrichum* are white, whereas all others within the *S. tuberosum* complex are said to be pink (León and Alain 1957; Dietrich 1983; Dietrich 1984).

The type specimen of *S. droseroides* was cited as a Ramón de la Sagra specimen from the de Candolle herbarium (at G), of which a duplicate is presumed to have been given to Nees. The label of the holotype at G has separate annotations matching the handwriting of Nees (as “*Stenandrium droseroides*”) and de Candolle (as “Ramon de la Sagra”). The label of the isotype at GZU bears the handwriting of Nees. The label of the probable isotype at P matches the handwriting of de Candolle. The variability in leaf size and pubescence on the isotype specimen of *S. droseroides* at P is noteworthy. The specimen also erroneously contains a label for *Crescentia cucurbitina* L. collected by Charles Wright which is not present on the sheet.

**6a. *Stenandrium droseroides* subsp. *droseroides*.**

**6b. *Stenandrium droseroides* subsp. *longibracteatum*** H. Dietr., Wiss. Zeitschr. Friedrich-Schiller Univ. Jena, Math.-Naturwiss, Reihe 32:851. 1983. **TYPE.**— CUBA. **Matanzas:** Mpio. Varadero, lomas de Camarioca al sur de cantel, suelo serpentinoso, 19 Jul 1977, *Bisse et al. Fl. de Cuba 35002* (holotype: HAJB; isotype JE).

**DISCUSSION.**— This subspecies has been reported only from Cuba. The bracts of *Stenandrium droseroides* subsp. *longibracteatum* were described as being 12–14 mm long (Dietrich 1983).

**7. *Stenandrium heterotrichum*** Borhidi, Acta Bot. Acad. Sci. Hung. 23:316. 1978. **TYPE.**— CUBA. **Guantánamo:** Playa Aguacate cerca de Maravi, O. de Baracoa, 10 Apr 1960, *López Figueiras 586* (holotype: SV [incorporated by HAC]; isotype: BP).

**DISCUSSION.**— *Stenandrium heterotrichum* is endemic to Cuba. The protologue mentions peduncles 1–1.5 mm wide and leaves with short and long hairs (Borhidi and Muñiz 1978) suggestive of an affinity with *S. bracteosum* and *S. carolinae* from the Bahamas (cf. Correll and Correll 1982). Corollas of *S. heterotrichum* are white.

**8. *Stenandrium ovatum*** Urb., Symb. Antill. 9:129. 1923. **TYPE.**— CUBA. **Pinar del Río:** Prope Herradura, in pinetis arenosis, 10 Apr 1920, *Ekman 10701* (lectotype, designated here: S [05-310]; isoelectotypes: NY, US). Figure 4F.

**DISCUSSION.**— *Stenandrium ovatum* is endemic to Cuba. Its leaves were characterized as rounded to truncate at the base to distinguish it from others in the *S. tuberosum* complex with obtuse to cuneate leaf bases (León and Alain 1957).



9. *Stenandrium pallidum* H. Dietr., Wiss. Zeitschr. Friedrich-Schiller Univ. Jena, Math.-Naturwiss. Reihe 32:850. 1984 (“1983”). **TYPE.**— CUBA. **Guantánamo:** Mpio. San Antonio del Sur, Abra de Mariana, loma al oeste del barranco, 9 Feb 1979, *Bisse et al. Fl. de Cuba 39098* (holotype: HAJB; isotypes: B, JE).

**DISCUSSION.**— *Stenandrium pallidum* is endemic to Cuba. Dietrich (1983) characterized the species as having pubescent sepals and bracts 7–8 mm long.

10. *Stenandrium pinetorum* (Britton & P. Wilson) Alain [Liogier], Rev. Soc. Cub. Bot. 13:9. 1956. *Gerardia pinetorum* Britton & P. Wilson, Bull. Torrey Bot. Club, 43:466. 1916. **TYPE.**— CUBA. **Isla de la Juventud [“Isla de Pinos”]:** Along Los Indios River above Los Indios, 21 May 1910, *Jennings 456* (holotype: NY). Figure 4B.

**DISCUSSION.**— *Stenandrium pinetorum* is endemic to Cuba. The holotype of *Gerardia pinetorum* was annotated by Emery C. Leonard as *S. tuberosum* in 1931. León and Alain (1957) characterized *S. pinetorum* as having entire to occasionally repand leaves with obtuse to cuneate bases, acuminate bracts 4–5 mm, ciliolate calyx lobes, and pink corollas.

11. *Stenandrium tuberosum* (L.) Urb., Symb. Antill. 4:576. 1911. *Gerardia tuberosa* L., Sp. Pl. 2:610. 1753. **TYPE.**— Lectotype (designated here): Plumier’s illustration in Burman, Pl. Amer., fas. 3, tab. 75, fig. 2. 1756. Figure 4A.

*Ruellia rupestris* Sw., Fl. Ind. Occid. 2:1071. 1800. *Stenandrium rupestre* (Sw.) Nees in Alph. de Candolle, Prodr. 11:283. 1847. **TYPE.**— “Habitat in fissuris rupium juxta fluvios in desertis Hispaniolae,” *Herb. Swartz* (holotype: S [R-5514]; probable isotype: S [R-5515]).

*Gerardia portoricensis* Britton & P. Wilson, Sci. Surv. Porto Rico & Virgin Islands 6:214. 1925. **TYPE.**— PUERTO RICO. **Guánica:** Salinas de Guánica, limestone hills, 7 Mar 1925, *Britton et al. 8288* (holotype: NY).

**DISCUSSION.**— *Stenandrium tuberosum* has been recognized as part of the flora of Cuba (León and Alain 1957), Hispaniola (Moscoso 1943; Liogier 1995), Puerto Rico (Liogier 1997), the Virgin Islands, and the Lesser Antilles (Acevedo-Rodríguez and Strong 2012). *Stenandrium rupestre* was treated as a synonym by Sprengel (1825), Urban (1911), Jennings (1917), León and Alain (1957) and Liogier (1997); *Gerardia portoricensis* was treated as a synonym by Liogier (1997). The holotype of *G. portoricensis* was annotated by Emery C. Leonard as *S. tuberosum* in 1931.

*Stenandrium* Nees subgen. *Coriifolium* H. Dietr., Wiss. Zeitschr. Friedrich-Schiller Univ. Jena, Mat.-Naturwiss 32:854. 1984. **TYPE.**— *Stenandrium wrightii* Lindau (1900:208).

**DISCUSSION.**— This subgenus includes *Stenandrium ekmanii* Urb., *S. scabrosum* Nees, *S. undulatum* Urb. & Ekman, and *S. wrightii* Lindau from the West Indies. *Stenandrium nanum* (Standl.) T.F. Daniel from the Yucatán (Daniel 1984) has similarly coriaceous leaves and may also pertain to this subgenus.

#### Key to species of *Stenandrium* subg. *Coriifolium* in the West Indies

- 1b. Plants rosulate, internodes inconspicuous. . . . . 2
- 1a. Plants caulescent, internodes conspicuous . . . . . 3
- 2a. Leaves > 9 cm long, blades abaxially punctate-pitted but lacking protuberances or trichomes; inflorescences > 30 cm long . . . . . 1. *S. ekmanii*

- 2b. Leaves up to 9 cm long, blades abaxially scabrous with subconic protuberances usually terminated by eglandular trichomes and pubescent along midvein; inflorescences up to 26 cm long  
..... 2. *S. scabrosum*
- 3a. Leaf blades crenate, > 2 cm long; stem internodes > 8 mm long; inflorescences > 8 cm long .  
..... 3. *S. undulatum*
- 3b. Leaf blades entire, < 2 cm long; stem internodes < 6 mm long; inflorescences up to 8 cm long  
..... 4. *S. wrightii*

1. *Stenandrium ekmanii* Urb., Symb. Antill. 9:130. 1923. **TYPE.**— CUBA. **Guantánamo:** Prope Bayate, Picote, in cacumine montis calcarei, in declivibus saxosis umbrosis, 550 m, flowers white, 16 Jul 1916, *Ekman 7407* (lectotype, designated here: S [05-308]; isolectotypes: BM, GH, US). Figure 5D.

*Stenandrium glabrescens* Urb., Symb. Antill. 9:131. 1923. **TYPE.**— CUBA. **Holguín:** In Sierra de Nipe ad Río Piloto, 14 Mar 1915, *Ekman 5021* (lectotype, designated here: S [05-309]; isolectotypes: NY, US).

**DISCUSSION.**— *Stenandrium ekmanii* is endemic to Cuba (Acevedo-Rodríguez and Strong 2015), and was erroneously reported in South America (Acevedo-Rodríguez and Strong 2012; IPNI 2013). *Stenandrium glabrescens* was treated as a synonym by León and Alain (1957).

2. *Stenandrium scabrosum* (Sw.) Nees in Alph. de Candolle, Prodr. 11:284. 1847. *Ruellia scabrosa* Sw., Fl. Ind. Occid. 2:1074. 1800. **TYPE.**— “Habitat in petrosis umbrosis Hispaniolae,” *Herb. Swartz* (holotype: S [R-5516]; probable isotype: S [S09-8408]). Figure 5B.

*Stenandrium punctatum* Griseb., Cat. Pl. Cub. 196. 1866. *Stenandrium scabrosum* (Sw.) Nees subsp. *punctatum* (Griseb.) Borhidi, Bot. Közelm. 62:27. 1975. **TYPE.**— CUBA. **Holguín:** Mata, La Catalina, nr. Sagua de Tánamo, *Wright 3062* (holotype: GOET; isotypes: GH, K!, MO!, NY, P, S [09-8643], YU).

**DISCUSSION.**— *Stenandrium scabrosum* occurs in Cuba and Hispaniola. *Stenandrium punctatum* was regarded as a synonym by Lindau (1900), León and Alain (1957), and Wasshausen (annotation of holotype in 1975), but it was recognized as a subspecies without comment by Borhidi and Muñiz (1975). Howard (1988) provided locality information for Wright’s type collection of *S. punctatum*.

3. *Stenandrium undulatum* Urb. & Ekman, Ark. Bot. 22A:92. 1928. **TYPE.**— HAITI. **Artibonite:** Massif du Nord, Ennery, top of Morne Perroy, limestone crags, 1075 m, 13 Jun 1927, *Ekman H-8437* (lectotype, designated here: S [05-313]; isolectotypes: A, CAS!, F, G, K!, NY, S [05-312], US). Figure 5A.

**DISCUSSION.**— *Stenandrium undulatum* is endemic to Haiti.

4. *Stenandrium wrightii* Lindau, Symb. Antill. 2:208. 1900, non *Gerardia wrightii* A. Gray (1859). *Gerardia consobrina* S.F. Blake, Contr. Gray. Herb. 52:100. 1917. **TYPE.**— CUBA. **Guantánamo:** Prope villam Monte Verde dictam, Jan–Jul 1859, *Wright 1344* (lectotype, designated here: GOET; isolectotypes: GH, K!, MO!, NY, P, S [09-8653, 09-8655], UC!, US). Figure 5C.

**DISCUSSION.**— *Stenandrium wrightii* is endemic to eastern Cuba. If a type specimen existed at B, it was destroyed. The specimen at GOET bears the handwriting of Lindau and is designated as the lectotype.

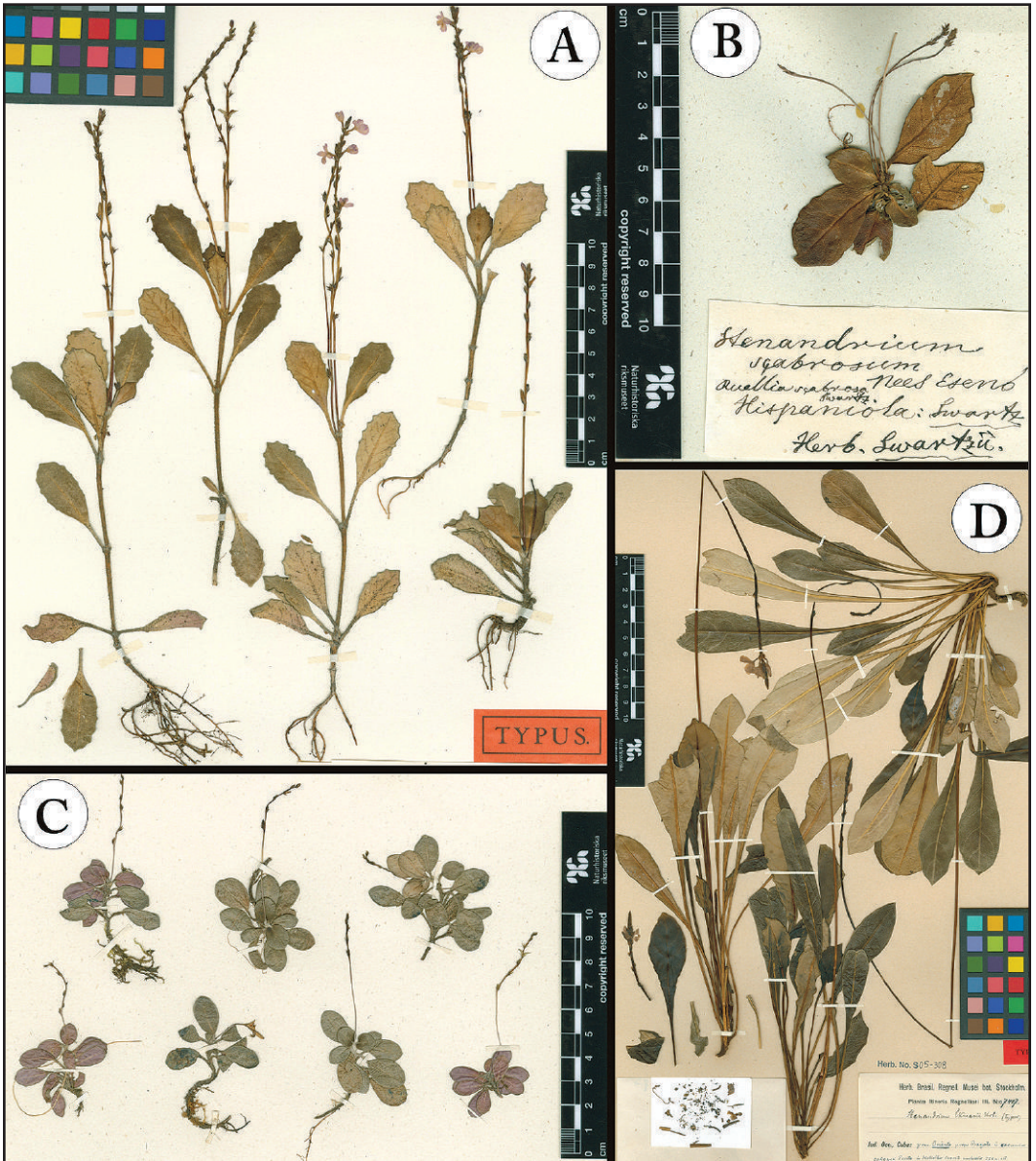


FIGURE 5. A. Lectotype of *Stenandrium undulatum*, Ekman H-8437 [05-313]. B. Holotype of *Stenandrium scabrosum*, Herb. Swartz [R-5516]. C. Lectotype of *Stenandrium wrightii*, Wright 1344 [09-8655]. D. Lectotype of *Stenandrium ekmanii*, Ekman 7407 [05-308]

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## Appendix

Specimens examined (other than types) organized by taxon, country (or island if country unknown), and collector. Specimens studied in person are marked with an exclamation mark, whereas those examined from digital photos are unmarked.

**Barleriola inermis.** DOMINICAN REPUBLIC: *García & Jiménez 4257* (FTG!); *Jiménez 761* (JBSD).  
**B. satirejoides.** CUBA: *Alvarez & Areces 29491* (FTG!); *Britton et al. 12633* (K!); *Ekman 15617* (P); *Linden s.n.* (P). **B. solanifolia.** CUBA: *Acuna 4427* (P); *Bonpland s.n.* (P); *Combs 88* (K!); *de la Sagra 437* (G); *Eggers 4850* (K!, P); *Howard 4838* (P); *Jack 5498* (K!, P), 5596 (CAS!); *Morton & Acuna 3410* (K!, UC!); *Otto 134* (K!), *s.n.* (K!, P); *Poeppig s.n.* (K!); *Wright 1342* (K!), 3058 (K!, P). DOMINICAN REPUBLIC: *Eggers 1787* (K!); *Ekman 13092* (K!); *Fuertes 406* (K!, P); *Howard & Howard 8813* (P); *Liogier 14366* (P); *Schomburgk s.n.* (K!); *von Türckheim 2699* (K!, P); *Valeur 861* (K!); *Veloz & Peguero 3942* (FTG!). HAITI: *Leonard 9890* (UC!). HISPANIOLA (“St. Domingue”): *Bonpland s.n.* (P); *Jacquemont s.n.* (P); *Schomburgk 38* (P); *Voranue s.n.* (P). PUERTO RICO: *Proctor 45499* (FTG!). **Salpicantha coccinea.** JAMAICA: [*Anonymous s.n.*] (GZU); *Abdo et al. 3104* (FTG!); *Adams et al. 10887* (UCWI!); *Alexander s.n.* (K!, NY); *Britton 727, 2307* (NY); *Davis s.n.* (UCWI!); *duQuesnay 255* (UCWI!); *Fawcett & Harris 7018* (UCWI!); *Goodfriend s.n.* (UCWI!); *Goodfriend & Tanner 2302* (UCWI!); *Harris 8163* (UCWI!), 8873 (K!, UCWI!), 10301 (K!, UCWI!), 12861 (CAS!, K!, UCWI!); *Henry s.n.* (UCWI!); *Hooker s.n.* (GZU); *Kelly 8010* (TCD!); *Purdie s.n.* (K!, TCD!); *Proctor 11046* (BM); *Proctor 36692* (FTG!); *Raz et al. 759* (FTG!); *Webster & Proctor 5635* (BM); *Wilson 135* (K!). **S. purdieana.** JAMAICA: *Adams 6801* (UCWI!); *Burch & Proctor 7123* (USF!); *Harris 10669* (C, K!, NY, P, UCWI!); *Howard & Proctor 14382* (FTG!, NY); *Lewis 324–327* (UCWI!); *Perkins 1337* (K!); *Proctor 20760* (BM, NY); *Proctor 34720* (BM, NY, USF!). **Sapphoa ekmanii.** CUBA: *Ekman 3844* (S). **S. rigidifolia.** CUBA: *Ekman 15975* (G, S [Fig. 2C]). **Stenandrium acuminatum.** HAITI: *Ekman 10276* (K!). **S. bracteosum.** BAHAMAS: *Correll & Popenoe 42637* (FTG!); *Wilson 7440* (NY). **S. carolinae.** TURKS & CAICOS: *Correll 43393* (FTG!); *Manco s.n.* (FTG!); *Sadle & Trusty 269* (FTG!). **S. crenatum.** CUBA: *Ekman 15462* (K!, UC!). **S. droseroides.** BAHAMAS: *Correll & Popenoe 42636* (FTG!); *Correll & Wasshausen 52075* (CAS!), 52080 (CAS!, FTG!); *Correll et al. 51113-B* (FTG!); *Linden 1991* (K!); *Proctor 30584* (FTG!); *Wunderlin et al. 8554* (USF!). CUBA: *Britton et al. 696* (NY), 6156 (NY), 6456 (NY), 7115 (NY), 14398 (NY), 15697 (NY); *Combs 492* (K!, P); *Curtiss 454* (K!, MO!, P); *Howard 5543* (P); *Howard et al. 435* (UC!); *Ledin s.n.* (FTG!); *León & Roca 8171* (NY); *Linden 1991* (P); *Shafer 3173* (NY); *Wright 3061* (K!, NY, P, UC!). DOMINICAN REPUBLIC: *Canela 189* (P). **S. ekmanii.** CUBA: *Ekman 15083* (K!, BM, UC!). **S. ovatum.** CUBA: *Ekman 14080* (K!, P, UC!). **S. pinetorum.** CUBA: *Killip 45669* (P). **S. scabrosum.** CUBA: *Shafer 3919, 7844* (NY). DOMINICAN REPUBLIC: *Liogier 16510* (P). HAITI: *Ekman 10774* (K!); *Eyerdam 315* (MO!, P). HISPANIOLA (“Santo Domingo”): *Eggers 2592* (K!). **S. tuberosum.** CUBA: *Wright 3060* (K!). DOMINICAN REPUBLIC: *Canela 787* (P); *Liogier 15894, 16297* (P); *Valeur 762* (K!). HAITI: *Ekman 4498* (P); *Eyerdam 266* (MO!, P). HISPANIOLA (“Sto. Domingo”): *Eggers 2332* (K!). PUERTO RICO: *Brecken s.n.* (MAPR); *Liogier 10167* (NY); *Liogier et al. 30849* (NY); *Shafer 3023* (NY); *Sauleda et al. 7692* (USF!); *Sintenis 702a* (K!), 2459 (P); *Woodbury s.n.* (NY). ST. THOMAS: *Eggers 494* (CAS!, P); *Urban 2459* (K!). **S. wrightii.** CUBA: *Howard 5870* (P); *Wright 1344* (UC!).

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## A Phylogenetic Overview of Sponge-inhabiting Barnacles and Their Host Specificity (Crustacea, Cirripedia)

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The subfamilies Acastinae and Bryozobiinae and the genus *Membranobalanus* are three groups of barnacles (Cirripedia: Archaeobalanidae) with species known to be obligate symbionts of Porifera. Few studies have attempted to identify both sponge and barnacle taxa in these relationships. Even less is known regarding the species-level specificity of the relationships.

Taxonomic data from identified specimens sampled at the Porifera collection of the Queensland Museum is compiled with sponge identifications made from the sponge-inhabiting barnacles in the Cirripedia collection at the California Academy of Sciences. The combined dataset of barnacle taxa and their sponge hosts is examined for host specificity for barnacle species, genera and subfamily levels.

The sponge symbiont species in the subfamily Acastinae live in a broad range of Porifera (at least 81 species of Porifera from several different orders). However, barnacle species in *Membranobalanus* are almost always obligate symbionts of clonoid sponges, and all but one genus in the Bryozobiinae are only found with *Clathria* sp. (Microcionidae). *Bryozobia* was originally believed to be a symbiont of the calcareous bryozoan on which it was discovered (Ross and Newman 1996), but more recently published data show it to be an obligate symbiont of *Clathria* sp. growing in or on calcareous substrata (Van Syoc and Newman 2010). All known Bryozobines inhabit thin, encrusting sponges. This enables them to maintain a tenuous contact with the substratum beneath the sponge.

Cirripedia were first described in association with Porifera by Poli (1791). In 1817 Leach proposed the genus *Acasta* to accommodate the sponge-inhabiting barnacles. Darwin (1854) revised the group and added descriptions of four living species of *Acasta* to the four species known prior to that time. Since then, many new species of Porifera-inhabiting Cirripedia have been discovered and described. However, often the host sponge taxon was not well defined. Kolbasov (1993) studied the sponge collections of Koltun (Zoological Institute, St. Petersburg, Russia), determining host sponge species relationships for many species of described Acastinae, as well as several new species of barnacles. Nearly all of the known species of sponge-inhabiting barnacles are in the family Archaeobalanidae. Most are in the subfamily Acastinae, with others in the subfamily Bryozobiinae and the genus *Membranobalanus*.

As with many other marine taxa, sponge-inhabiting barnacles are most numerous and diverse in the coral reef habitats of the tropics. SCUBA equipped scientists, using hand collecting tech-

niques (Fig. 1), can select and collect sponges in a manner that enables accurate taxonomic analysis for both the sponge and their barnacle symbionts. Using new collections made with SCUBA, as well as those in museum collections built largely through the efforts of diving scientists, allows us to more fully explore both barnacle and sponge diversity and host-specificity. Additionally, appropriate preservation of specimens or tissues to stabilize DNA molecules permits molecular level taxonomic comparisons to morphological data.

The subfamily Acastinae was first defined by Kolbasov (1993) as Archaeobalanidae with six solid wall plates with solid radii; a cup-shaped, rarely flat or elongated, calcareous or membranous basis; and cirri with segments of anterior rami of III and IV with hooks or “thorns”, or rarely without armature. In addition, we note that Acastinae have spines or projections of various length on the parietes. These may be small bumps on the surface, short pointed, or long hollow calcareous growths extending away from the parietes. They often breakaway from the shell wall when the barnacle is removed from the host sponge, leaving behind circular holes in the shell wall marking the site of attachment (Fig. 2). The Acastinae with membranous bases may often be distinguished from *Membranobalanus* spp. by the presence of these calcareous projections, or the “pores” left behind when they are broken off the shell wall. Although nearly all Acastinae have fully calcified bases, some species exhibit remnants of light calcification in a mostly membranous basis, whereas in others the basis is completely membranous. This suggests that the membranous basis is secondarily derived from the partially calcified state.

Sixty-one described species of Acastinae inhabit sponges, in addition 12 species have been described as symbionts of either octocorals (e.g., *Acasta vipensis* Van Syoc et al., 2014) or antipatharia (e.g., *Acasta antipathidis* Broch, 1916).

Only two species of non-archaeobalanid barnacles are known to have associations with sponges. *Pyrgospongia stellula* (Rosell, 1973) is the only species in the family Pyrgomatidae to inhabit sponges. Achituv and Blecher (2006) noted several differences between *Pyrgospongia stellula* and the other pyrgomatids. They suggest that it “might be supposed that *Pyrgospongia* was derived from within *Cantellius*.” They also note that it “may not be a pyrgomatid at all.” But they offer no alternative family assignment. Presumably, the Archaeobalanidae would be the most appropriate alternative. The remainder of the Pyrgomatidae inhabit scleractinian corals. Rosell (1973) noted that he found specimens of “*Membranobalanus orcutti*” in the same “calcareous



FIGURE 1. Diving in the Verde Island Passage, Philippines. Biologists using SCUBA collecting techniques to sample coral reef inhabiting organisms for a biodiversity study in the Philippines. Photo: Gary C. Williams.

sponge” as his type material of *Pyrgospongia stellula* (formerly *Pyrgopsella stellula*). It is possible that the “calcareous sponge” may be a species of Clionaidae, as they commonly burrow into calcareous substrata.

The other non-archaeobalanid species inhabiting sponges appears to have a facultative relationship with its host. *Balanus rostratus apertus* Pilsbry, 1916, a northeast Pacific species in the Balanidae, is a form of *Balanus rostratus* that develops a distinct morphology when embedded within the tissues of the hexactinellid sponge *Aphrocallistes vastus*. Given the distinct morphology and the specialized habitat of this form, it may yet be shown to be genetically differentiated from the free-living forms of *Balanus rostratus*.

## METHODS

One of us (RJVS) examined the Queensland Museum Porifera (QMP) collection for Cirripedia. The barnacle taxa were identified to basic morpho-species level using shell wall and basis characters. Most of the barnacle taxa appear to be undescribed species. Additional samples of sponge-inhabiting Cirripedia were discovered in the field and within the collections at the California Academy of Sciences (CASIZ). Porifera hosts for these samples were identified by RWMVS and JRX. Finally, additional barnacle-sponge host relationships were taken from those original descriptions that mention host sponge taxa (many do not) and other subsequent references, especially Kolbasov’s (1993) revision of *Acasta*. For such records sponge names were verified against the World Porifera Database (WPD, van Soest et al. 2015) and, whenever applicable, changed to the currently accepted names.

Some published records were discounted as inaccurate due to the probability of incorrect identification of barnacle species. This interpretation was generally applied for names used for specimens collected in ocean basins other than that of their type locality. For example, the name *Acasta cyathus* has been used for samples collected from the Caribbean Sea, Atlantic Ocean, Red Sea, Western Pacific Ocean, and Indian Ocean. However, the recognized type locality of *Acasta cyathus* is the Caribbean/Western Atlantic. Other records from localities in other ocean regions are questionable. Although some barnacle taxa commonly foul ships and are easily dispersed through

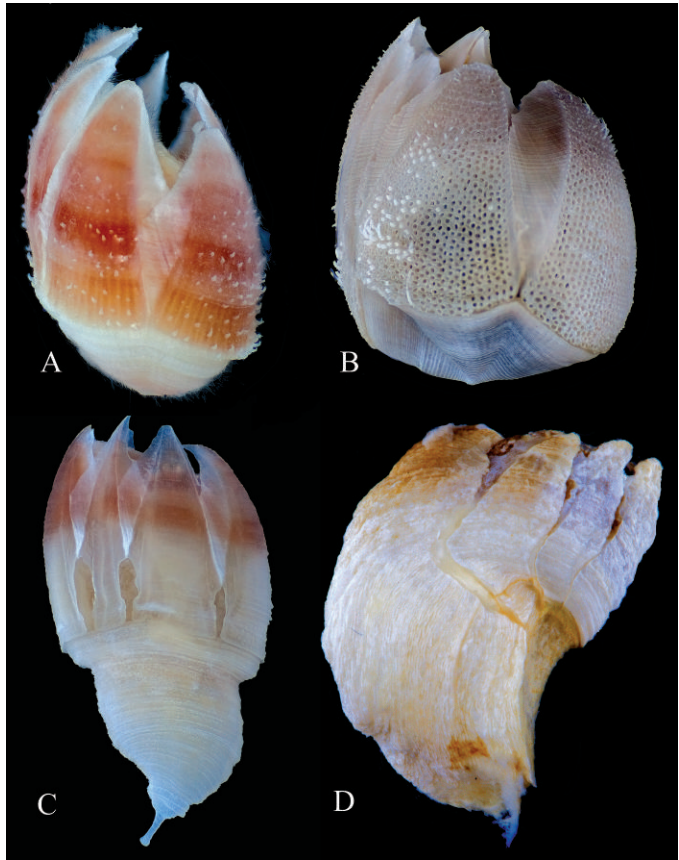


FIGURE 2. Examples of Acastinae and *Membranobalanus* shell morphology. (A) CASIZ 179563, *Acasta* sp., host sponge, *Clathria* (*Thalysias*) aff. *cratitia*, ZMAPOR 21932; (B) CASIZ 179566, *Acasta* sp., host sponge, *Aaptos suberitoides*, ZMAPOR 21935; (C) CASIZ 179564, *Acasta* sp., host sponge, *Acanthostrongylophora ingens*, ZMAPOR 21933 (D) CASIZ 166611, *Membranobalanus declivus*, host sponge, *Spheciospongia vesparium*.

human activities, species that are obligate symbionts of sponges are not candidates for this type of dispersal. In addition, larval dispersal is generally limited to exchange within recognized oceanic bioregions, e.g. Caribbean/Western Atlantic, Eastern Atlantic, Eastern Pacific, Western Pacific, and so forth. This is especially true for tropical and warm temperate species that are restricted from the cooler seas of the polar regions and so prevented from spreading across the northern Pacific and Atlantic Oceans. Therefore, we have included the many records Kolbasov (1993) listed for *Acasta cyathus* from the Indian Ocean as *Acasta* “*cyathus*”. Similarly, we have filtered the wide spread records for *Eoacasta dofleini*. Given the number of host taxa listed by Kolbasov (1993), these wide spread records of *E. dofleini* may represent a closely related group of barnacle species that are morphologically similar in some respects. Ilan et al. (1999) note that both *E. dofleini* and *A. cyathus* are “variable species” morphologically. It seems likely these represent species complexes rather than single species inhabiting a large number of taxonomically diverse host taxa. However, an alternative hypothesis offered by Kolbasov (1993, and also Ilan et al. 1999) suggests instead that these two species have evolved to live in several disparate sponge taxa and limit their contact with sponge tissues with more complete calcification than barnacles exhibiting greater host specificity.

**MOLECULAR METHODS.**— Genomic DNA was extracted from barnacle adductor muscle tissue using the Qiagen DNeasy Blood and Tissue kit (Valencia, CA). The cytochrome c oxidase subunit I (COI) primers COI-N: TGAGAAATTATTCCGAAGGCTGG (Van Syoc 1994, 1995) and LCO 1490: GGTCAACAAATCATAAAGATATTGG (Folmer et al. 1994) were used to amplify approximately 700 base pairs of the mitochondrial genome (mtDNA). Histone 3 primers H3F: ATG-GCTCGTACCAAGCAGACVGC and H3R: ATATCCTTRGGCATRATRGTGAC (Colgan et al. 1998) were used to amplify approximately 350 base pairs of the nuclear genome (nDNA). Sequence alignments were performed initially with Geneious Pro 5.6.4 (Kearse et al. 2012) and then edited by hand. Phylogenetic reconstructions were performed under maximum likelihood and Bayesian inference methods using PHYML 3.0 (Guindon et al. 2010) and Geneious Pro 5.6.4 (Kearse et al. 2012), respectively.

**MUSEUM COLLECTION NUMBER ACRONYMS.**— Queensland Museum, Porifera collection catalog numbers are preceded by the acronym QMP. California Academy of Sciences, Invertebrate Zoology collection catalog numbers are preceded by the acronym CASIZ. Zoological Museum of Amsterdam, Porifera collection catalog numbers are preceded by the acronym ZMAPOR.

## RESULTS AND DISCUSSION

The archaeobalanid subfamily Acastinae is by far the most taxonomically diverse of the sponge-inhabiting barnacle groups. Likewise, it exhibits the greatest diversity in sponge host taxa. Where known, these are listed in Appendix Tables 1 and 2. Host taxon identifications for published barnacle species are derived from original descriptions whenever possible. However, many original descriptions lack host sponge identifications.

The QMP collection survey yielded 87 different morpho-species of barnacles in sponge hosts from 9 orders, 23 families, 52 genera (some not identified to species level), and 43 identified (some undescribed) species. Sixty-nine barnacle morpho-species were extracted from only single sponge samples. They were not found in any of the other samples. However, 18 barnacle morpho-species were found in multiple sponge samples. Of these multi-samples, seven morpho-species inhabited multiple samples of a single species of sponge host, six were found in a single genus of sponge host, and three in a single family of host sponges. Only 2 of the 87 barnacle morpho-species in the QMP collection were not host specific at family level or below. About 21% of the barnacle morpho-species in the QMP collection were present in more than one sponge sample, 89% of those in multiple samples are sponge host specific at the family level or below.

Kolbasov (1993) examined 26 species of sponge-inhabiting barnacles taken from the sponge collection of Prof. V.M. Koltun at the Zoological Institute, St. Petersburg, Russia. The barnacles in the Koltun collection were found in 9 orders, 16 families, and 14 genera of sponges. Some hosts are identified only to family level, others to genus level. None of the host sponges in Kolbasov (1993) are identified to species level. In addition, changes in Porifera taxonomy have taken place since 1993, resulting in the synonymizing of some families and genera. Kolbasov (1993) did not include the monotypic genus *Pseudoacasta*, *Pseudoacasta libera* Nilsson-Cantell, 1930, as a member of the Acastinae. The host of *Pseudoacasta libera* is unknown, Nilsson-Cantell (1930) suggested that it is probably a species of sponge.

Holmes (unpublished thesis, 2001) noted that *Membranobalanus acutus* Kolbasov, 1993 has many characters in common with the Acastinae. Kolbasov noted the membranous basis and somewhat extended basal margins of the carina and rostrum, as well as part of the latera as being characters of the genus *Membranobalanus*. However, several species of Acastinae have membranous bases, and Holmes further notes the calcareous spines on *M. acutus* (these are absent in all other *Membranobalanus* spp.). Additional morphological evidence is presented in a morphological cladistics analysis by Holmes that results in the clustering of *Membranobalanus acutus* with some other acastines with membranous bases. Therefore we are re-assigning this species, *Membranobalanus acutus* Kolbasov, 1993 (host sponge taxon, *Petrosia* sp.), to the genus *Acasta* and list it as *Acasta acuta* (Kolbasov, 1993) in the tables herein.

There is some evidence from morphology and DNA sequence data (CO1 and H3) for species-level host specificity, also some subgenus-level host specificity, closely related species of barnacles living in different sponge host species of the same genus.

The Acastinae is possibly a polyphyletic group, perhaps having evolved symbiosis more than once in different groups of sponges. The Bryozobiinae and *Membranobalanus* are more specific in their host requirements. Given this narrow range of specific host taxa, it is possible that these two groups evolved more recently from independent archaeobalanid lineages not directly related to the Acastinae. However, it is interesting to note that although some species of Acastinae are found in Microcionidae (typical hosts of bryozobines), they are not presently known from hosts in Clionaidae, the sponge taxon commonly (perhaps the only sponge taxon, see discussion on the findings of Ilan et al. 1999 below) inhabited by *Membranobalanus*.

Questions remain regarding the phylogenetic significance of host specificity. Acastinae have also adapted to living in various non-sponge hosts, including gorgonians, alcyonarians or antipatharians: do these cnidarian-inhabiting species form a monophyletic group, with the sponge-inhabiting Acastinae forming a sister group? Or do host taxon preferences reflect the independent evolution of polyphyletic groups of barnacles? Increasingly, evidence from trees built with DNA sequence data (Shuto, pers. comm.) points to polyphyly and multiple lineages of barnacles invading various sponge host taxa.

In contrast to the host diversity found among the Acastinae, all 10 described species of *Membranobalanus* Pilsbry 1916, are known from hosts in the family Clionaidae, eight in the genus *Cliona* spp., two in *Sphaciospongia* spp. *Membranobalanus* synapomorphies include a rostrum (and other wall plates in some cases) elongated with rounded basal margins and a membranous basis, not attached to substratum beneath sponge. In addition, they are lacking spines or other calcareous projections or knobs on the exterior of shell wall. These calcareous spines or projections are common in the Acastinae. However, some Acastinae have apparently lost their calcareous basis and now exhibit a partially or fully decalcified, membranous basis. This has led to some taxonomic confusion regarding the difference between *Membranobalanus* and the Acastinae. The host sponge taxon would appear to offer an independent line of evidence supporting the hypothesis that

lightly calcified sponge-inhabiting barnacles possessing spines on parietes belong to the Acastinae, regardless of the degree of calcification of the basis.

Ilan et al. (1999) studied host sponge specificity of barnacles from the Red Sea. They found seven species of Acastinae in seven families, and eight genera of sponges. They also found *Membranobalanus longirostrum* in a sponge they identified as *Suberites* cf. *clavatus*. If it is indeed a specimen of *Suberites*, this would be the only record of *Membranobalanus* in a non-clionaid sponge host. However, a similar sponge species, *Spheciospongia vagabunda*, is known from the Red Sea and *Spheciospongia* spp. are known to host *Membranobalanus longirostrum*. Given the host specificity shown by *Membranobalanus* to the family Clionaidae, and the potential difficulty in distinguishing these sponge taxa using external morphology, we think it's possible that an error was made in the identification of this sponge host in Ilan et al. (1999). However, the possibility remains that some membranobalanids live with suberitid sponges. We have listed this relationship as Ilan et al. (1999) published it, with the footnote that the host may rather be *Spheciospongia vagabunda*.

Kolbasov's (1993) hypothesis regarding barnacles with greater membrane exposure to sponge tissue suggests they would be more host specific than those with great calcification. Certainly, it seems to be true for *Membranobalanus*, in which all of the species have membranous bases. There may be other reasons for this specific relationship with burrowing sponges. *Membranobalanus* individuals may derive a special benefit from their close association with clionoids. There may be a transfer of chemical compounds across the membrane barrier between barnacle and sponge that benefits one or both partners. Perhaps the barnacles are able to absorb and utilize carbonates dissolved by the sponge as it burrows through its calcareous substratum.

Adaptations of sponges to "burrowing" into or encrusting the surface of calcareous substrata also favors the potential of the chance association with early ancestors of symbionts. Any barnacles settling on calcareous substrata could be overgrown by neighboring sponge. This would appear to be the case with bryozobines, a group of Cirripedia that have evolved complex calcareous structures to accommodate their life with sponge hosts.

The Bryozobiinae possess a variety of atria and portals (Figs. 3 and 4) that were originally thought to accommodate bryozoan hosts, however we now recognize that the five genera and 9 species of bryozobines now known all inhabit sponge hosts (Van Syoc and Newman, 2010). We have a very small sample size, six host samples, however there appears to be a host taxon preference for bryozobiines. This preference appears at the genus level for barnacles and encrusting sponge hosts growing on calcareous substrata (e.g. dead coral, bivalve shells). As with the Acastinae, no Bryozobiinae are found in sponge hosts in the family Clionaidae. Again, this family of sponges is inhabited only by the genera *Membranobalanus* and *Pyrgospongia*. The one *Pyrgospongia* sample from the QMP collection inhabits the clionaid sponge *Spheciospongia vagabunda*, from Malaysia (see Tables 1 and 2).

A cladistic analysis of the Bryozobiinae, based on 17 morphological characters (Fig. 5), indicates that *Clathria* (Microcionidae) sponges may be the most commonly inhabited hosts, with a derived host symbioses in *Monanchora* (Crambeidae) for the genus *Multatria*. The host taxon of *Poratria* is uncertain due to a poorly preserved sponge sample.

A Bayesian analysis derived phylogenetic tree from CO1 and H3 sequence data for sponge-inhabiting barnacle samples (Fig. 6) yields three clades corresponding to barnacles and their sponge host taxa. Clade A (blue-shaded box) contains four species of Acastinae from the Philippines and Madagascar in Phyllosponginae hosts. This shows host specificity at subfamily level for this clade with a global span of host specificity with a barnacle species from Madagascar clustering with three species from the Philippines, all inhabiting Phyllosponginae. The barnacles in this

clade also have several morphological synapomorphies that unite them.

Clade B (orange-shaded box) consists of three genera of Bryozobiinae barnacles from Madagascar in encrusting sponge hosts *Clathria (Microcionia)* sp. and *Monanchora* aff. *unguiculata*. Although these bryozobines cluster together, only two of the three genera inhabit *Clathria* host species. We lack DNA sequence data for other bryozobine species, so we are unable to extend the geographic coverage of the taxon in this phylogram, but specimens of *Multatria filigranus* from Palau also inhabit *Monanchora unguiculata*. So again we see broad geographic reach in host taxon specificity for related barnacle species.

Clade C (purple-shaded box) includes an undescribed species of *Eoatria* (Bryozobiinae) and three undescribed Acastinae barnacles in three different species of encrusting sponges, *Clathria (Microcionia)* sp. from Madagascar, *Clathria (Thalysias)* spp. and *Hymedesmia dichela* from the Philippines. Although we see some possible morphological

synapomorphies for the species in this clade, it may be that this group will not remain coherent with the addition of more taxa and other genes. In particular, the 3 species we now place in the Acastinae may yet form a clade to the exclusion of *Eoatria*, the lone bryozobine in this branch of the tree.

## CONCLUSION

Phylogenetic analyses of some of the sponge-inhabiting Cirripedia taxa using DNA sequence data confirm the concordance of barnacle and sponge host taxon relationships. Additional phylogenetic work and chemical ecological studies of the Porifera hosts have the potential to tell us more about the evolutionary ecology and history of these relationships. It is well known that barnacle larvae use chemical signals for settlement (Crisp 1974; Pawlik 1992; Nogata and Matsumura 2006), therefore it seems likely that sponge chemistry plays an important role in determining potential host taxa.

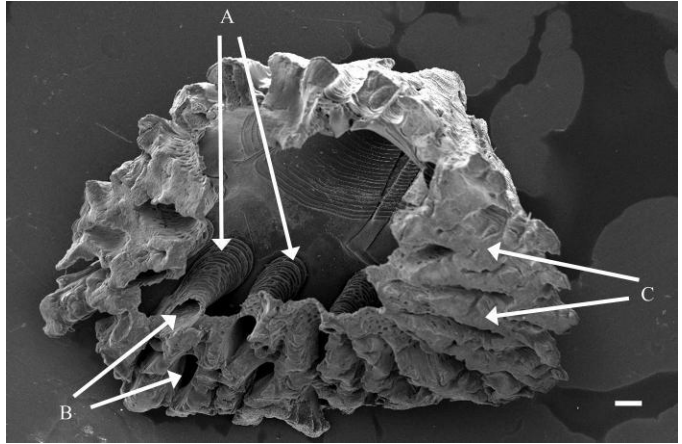


FIGURE 3. *Bryozobia synaptos*, complex basis and wall structures: atria (A), portals (B) and calcipecta (C) Basis attached to substratum, via calcipecta, beneath sponge. Scale bar equals 200  $\mu$ m.

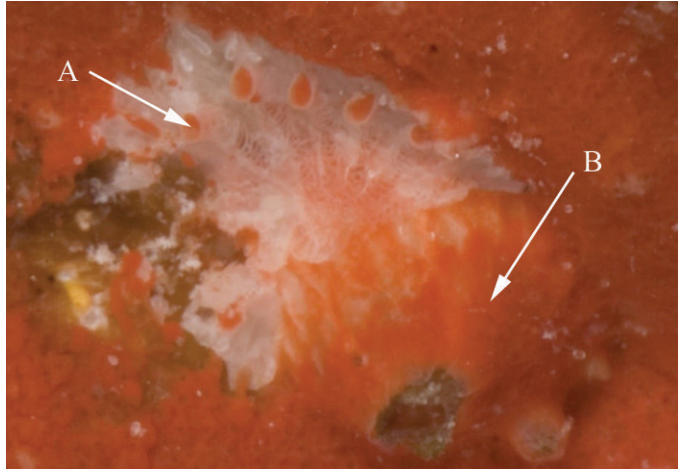


FIGURE 4. *Bryozobia synaptos* with red sponge *Clathria (Microcionia)* sp. from Madagascar. Host sponge is visible growing up through basal atria (tunnel, A) openings (portals, B) in barnacle shell. Photo: Terry Gosliner

Although we have only preliminary phylogenetic data for various sponge-inhabiting barnacles, there is evidence for some sponge host-taxon specificity at the barnacle morpho-species level. For example, *Acasta acuta* was only found in Petrosiidae sponges; *Acasta* sp. 9 was found only in Ancorinidae; *Acasta* sp. 14 only in *Cymastela*, and so on (Table 2). Additionally, at least some barnacle genera and clades of species show host taxon specificity at the sponge genus or sub-family level. All *Membranobalanus* spp. inhabit only sponges in the family Clionidae, most in the genus *Cliona*. Only one other barnacle taxon, *Pyrgospongia stellula*, has been found in a Clionidae sponge host. All Bryozobiinae barnacles inhabit encrusting sponge hosts. We have found them in species of *Clathria*, *Monanchora unguiculata* and *Hymedesia dichela*. None are symbionts of Clionidae. This preference for encrusting forms of sponges by the bryozobines fits nicely with their requirement to maintain basal attachment to a calcareous substratum, and being subsequently partially overgrown by their sponge symbiont (Van Syoc and Newman 2010).

The other barnacle taxa (tentatively placed in the Acastinae) clustering with *Eoatria* on the molecular phylogenetic tree live in encrusting sponge hosts, as do all Bryozobiinae barnacles. More detailed morphological analysis of this clade may reveal synapomorphies for the clade that ally them more closely to the Brozobiinae. Barnacle taxa currently assigned to the subfamily Acastinae inhabit a great number of sponge host taxa. If the Acastinae are polyphyletic, their host sponge taxa may reflect independent evolution of symbiotic relationships. Host specificity at the sponge genus or subfamily level may be used to explore barnacle lineages using new sets of morphological characteristics or, if suitable samples exist, DNA sequence data.

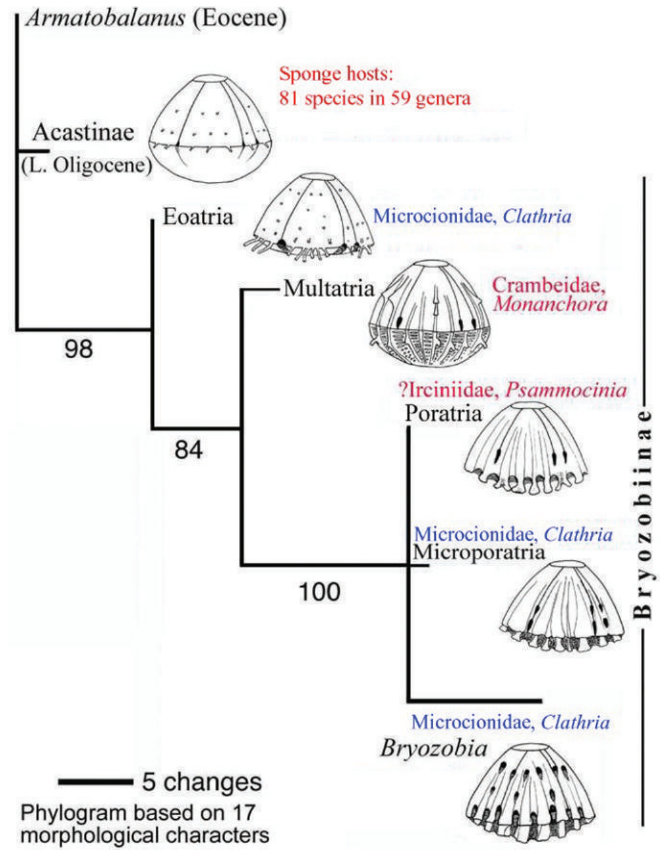


FIGURE 5. Phylogenetic tree for Bryozobiinae genera based on 17 morphological characters of the basis and wall plates. These barnacle genera are defined by the number and position of the atrial portals (openings) in wall plates. The more evolved forms have more atria and they are higher on the shell walls. *Eoatria* lacks pores in its atria. The atria of the other four genera of Bryozobiinae have pores of various number and size. Host sponge taxa are listed next to representations of barnacle taxa. (after Van Syoc and Newman 2010).

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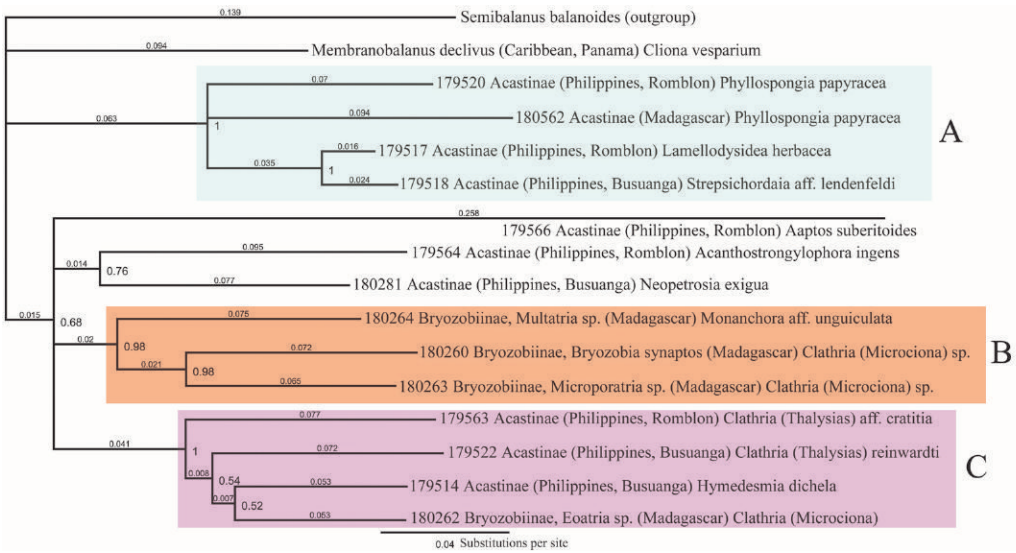


FIGURE 6. Bayesian phylogenetic tree based from CO1 and H3 concatenated sequence data (869 bp). Numbers at nodes represent Bayesian posterior probability values. Numbers on branches represent substitutions per site on that branch. (A) Clade of Acastinae from Philippines and Madagascar in Phyllospongiinae hosts (blue-shaded box); (B) Clade of Bryozobiinae (3 genera) barnacles from Madagascar in encrusting sponge hosts *Clathria* (*Microcionia*) sp. and *Monanchora* aff. *unguiculata* (orange-shaded box); (C) Clade of *Eoatria* sp. (Bryozobiinae) and 3 undescribed Acastinae barnacles in encrusting sponges (purple-shaded box). All barnacle taxa in this analysis are in the family Archaeobalanidae. All of the taxa identified as members of the Acastinae appear to be undescribed species. *Semibalanus balanoides* is used as the outgroup in the analysis and is not a sponge-inhabiting species. Numbers on taxon labels are CASIZ specimen catalog numbers.

pared many of the barnacle samples from the QMP collection. Ann Holmes' work on *Membranobalanus* helped shape our understanding of that genus relative to the Acastinae. Greg Kolbasov's pioneering work on host specificity in sponge-inhabiting barnacles forms a significant portion of the dataset herein. Our findings for host specificity of Bryozobiinae and *Membranobalanus* help support his ecological approach. The Philippines National Fisheries Research and Development Institute (NFRDI) facilitated specimen collecting in the Philippines that formed an essential part of this work. The Wildlife Conservation Society facilitated field work in Madagascar. The manuscript was improved by comments from John Buckeridge and an anonymous reviewer; however, any errors or omissions remain the responsibility of the authors.

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## **Appendix**

### **Tables 1 and 2**

TABLE 1. Sponge-inhabiting barnacles, their host sponges and references for host identifications. Sorted by sponge taxon. References are designated as Original Description, QMP, ZAMPOR, or CASIZ catalog numbers, or RVS field numbers, 1 = Kolbasov, 1993, 2 = Van Syoc & Winther, 1999, 3 = Ilan et al., 1999, 4 = Van Syoc & Newman, 2010.

Barnacle Genus	Barnacle Species	Sponge Order	Sponge Family	Sponge Genus	Sponge Species	Locality	Reference
Acacia	sp. 6	Agelasida	Agelasidae	Agelas	axifera Hentschel, 1911	WA	QM G300198
Acacia	sp. 6	Agelasida	Agelasidae	Agelas	mauritiana (Carter, 1883)	QLD	QM G304021
Acacia	sp. 76 and 78	Agelasida	Agelasidae	Agelas	mauritiana (Carter, 1883)	QLD	QM G314522
Acacia	crassa Broch, 1931	Agelasida	Agelasidae	Agelas		Indonesia	1
Acacia	sp. 9	Astrophorida	Ancorinidae	Melophlus		WA	QM G306165
Acacia	sp. 9	Astrophorida	Ancorinidae	Rhabdastrella	globostellata (Carter, 1883)	QLD	QM G300041
Acacia	sp. 9	Astrophorida	Ancorinidae	Rhabdastrella	globostellata (Carter, 1883)	QLD	QM G304884
Acacia	sp. 9	Astrophorida	Ancorinidae	Rhabdastrella	globostellata (Carter, 1883)	NT	QM G303634
Acacia	"cyanthus" Darwin, 1854	Astrophorida	Ancorinidae	unknown		Indian Ocean	1
Archiacasta	membranacea (Barnard, 1924)	Astrophorida	Pachastrellidae	Pachastrella	isorhopa Kirkpatrick, 1902	Southern Africa	Orig. descr.
Eucasta	"dofleini" (Kruger, 1911)	Astrophorida	Pachastrellidae	Pachastrella		Indian Ocean	1
Acacia	newmani Van Syoc & Winther, 1999	Astrophorida	Vulcanellidae	Pocellastra	tenuilaminaris (Sollas, 1886)	EPac, Mexico	2
Acacia	spongiformis Kolbasov, 1993	Astrophorida	Vulcanellidae	Pocellastra		Indian Ocean	1
Eucasta	"dofleini" (Kruger, 1911)	Clathrinida	Leuceitidae	Leuceitia		Indian Ocean	1
Acacia	"cyanthus" Darwin, 1854	Dietyoceratida	Dysideidae	Dysidea		Indian Ocean	1
Acacia	flexuosa Nilsson-Cantell, 1931	Dietyoceratida	Dysideidae	Dysidea		Indian Ocean	1
Acacia	spongites (Poli, 1791)	Dietyoceratida	Dysideidae	Dysidea		Indian Ocean	1
Neocasta	laevigata (Gray, 1825)	Dietyoceratida	Dysideidae	Dysidea		Indian Ocean, PNG	1
Neocasta	planibasis Kolbasov, 1993	Dietyoceratida	Dysideidae	Dysidea		Indian Ocean	1
Acacia	sp. A	Dietyoceratida	Dysideidae	Lamelldysidea	herbacea (Keller, 1889)	Philippines	CASIZ 179517, ZMAPOR 21746
Acacia	sp. 36	Dietyoceratida	Irciniidae	Ircinia		QLD	QM G304116
Archiacasta	fragilis (Ren, 1984)	Dietyoceratida	Irciniidae	Ircinia		S. China Sea	Orig. descr.
Archiacasta	hainanensis (Ren, 1984)	Dietyoceratida	Irciniidae	Ircinia		S. China Sea	Orig. descr.
Acacia	sp. 36	Dietyoceratida	Irciniidae	Psammocinia	bulbosa Bergquist, 1995	WA	QM G306050
Acacia	sp. 78	Dietyoceratida	Spongidae	Carterospongia	flabellifera (Bowerbank, 1877)	QLD	QM G317495
Acacia	sp. 80	Dietyoceratida	Spongidae	Hippospongia	cf. communis (Lamarck, 1814)	QLD	QM G305064
Acacia	collicata Kolbasov, 1992	Dietyoceratida	Spongidae	Spongia		Indian Ocean	Orig. descr.
Acacia	sp. 83	Dietyoceratida	Spongidae	Spongia		QLD	QM G303968
Eucasta	sporillus (Darwin, 1854)	Dietyoceratida	Spongidae	Spongia		Indian Ocean	1
Acacia	cyathus Darwin, 1854	Dietyoceratida	Spongidae	Spongia (Spongia)	tubulifera Lamarck, 1814	Caribbean, WAI	2
Neocasta	laevigata (Gray, 1825)	Dietyoceratida	Spongidae	unknown		Indian Ocean	1
Acacia	sp. 78	Dietyoceratida	Thorectidae	Carterospongia	cf. foliascens (Pallas, 1766)	WA	QM G306046
Acacia	sp. 78	Dietyoceratida	Thorectidae	Carterospongia	cf. foliascens (Pallas, 1766)	WA	QM G306164
Acacia	sp. 75	Dietyoceratida	Thorectidae	Carterospongia	flabellifera (Bowerbank, 1877)	QLD	QM G303017
Acacia	sp. 76	Dietyoceratida	Thorectidae	Carterospongia	flabellifera (Bowerbank, 1877)	QLD	QM G304114
Acacia	sp. 79	Dietyoceratida	Thorectidae	Dactylospongia		PNG	QM G312881
Acacia	sp. 80	Dietyoceratida	Thorectidae	Lendenfeldia	plicata (Esper, 1794)	QLD	QM G304093



TABLE 1 (continued). Sponge-inhabiting barnacles, their host sponges and references for host identifications. Sorted by sponge taxon. References are designated as Original Description, QMP, ZAMPOR, or CASIZ catalog numbers, or RVS field numbers, 1 = Kolbasov, 1993, 2 = Van Syoc & Winther, 1999, 3 = Ilan et al., 1999, 4 = Van Syoc & Newman, 2010.

Barnacle Genus	Barnacle Species	Sponge Order	Sponge Family	Sponge Genus	Sponge Species	Locality	Reference
Acacia	sp. 81	Dietyoceratida	Thorectidae	Phyllospongia	lamellosa (Esper, 1794)	QLD	QM G305424
Acacia	sp. 81	Dietyoceratida	Thorectidae	Phyllospongia	papyracea (Esper, 1794)	QLD	QM G303018
Acacia	sp. 82	Dietyoceratida	Thorectidae	Phyllospongia	papyracea (Esper, 1794)	QLD	QM G317706
Acacia	sp. B	Dietyoceratida	Thorectidae	Phyllospongia	papyracea (Esper, 1794)	Philippines	CASIZ 179519, ZMAPOR 21748
Acacia	sp. C	Dietyoceratida	Thorectidae	Phyllospongia	papyracea (Esper, 1794)	Philippines	CASIZ 179520, ZMAPOR 21749
Acacia	sp. D	Dietyoceratida	Thorectidae	Phyllospongia	papyracea (Esper, 1794)	MADAGASCAR	CASIZ 180562, ZMAPOR 21754
Acacia	sp. E	Dietyoceratida	Thorectidae	Strepsichordaia	aff. lendenfeldi Bergquist, Ayling & Wilkinson, 1988	Philippines	CASIZ 179518, ZMAPOR 21747
Acacia	sp. 80	Dietyoceratida	Thorectidae	Strepsichordaia	lendenfeldi Bergquist, Ayling & Wilkinson, 1988	QLD	QM G303910
Acacia	sp. 38	Dietyoceratida	Thorectidae	Thorecta		QLD	QM G300072
Membranobalanus	koreanus Kim & Kim, 1983	Hadromerida	Clionidae	Cliona	aff. celata Grant, 1826	S. Korea	Orig. descr.
Membranobalanus	occuti (Pilsbry, 1907)	Hadromerida	Clionidae	Cliona	aff. celata Grant, 1826	EPac, Mex, Calif	2
Membranobalanus	robiniae Van Syoc, 1988	Hadromerida	Clionidae	Cliona	raromiroscera (Dickinson, 1945)	EPac, Mexico	Orig. descr.
Membranobalanus	costatus Zullo & Standing, 1983	Hadromerida	Clionidae	Cliona	varians Duchassaing & Michelotti, 1864)	WAtl, N Carolina	Orig. descr.
Membranobalanus	brachialis (Rosell, 1972)	Hadromerida	Clionidae	Cliona		Philippines	Orig. descr.
Membranobalanus	cuneiformis (Hiro, 1936)	Hadromerida	Clionidae	Cliona		Japan	Orig. descr.
Membranobalanus	nebrisis (Zullo & Beach, 1973)	Hadromerida	Clionidae	Cliona		Galapagos Is.	Orig. descr.
Membranobalanus	sp. 1	Hadromerida	Clionidae	Sphectospongia	areolata (Dendy, 1897)	NSW	QM G301439
Membranobalanus	occuti (Pilsbry, 1907)	Hadromerida	Clionidae	Sphectospongia	confoederata de Laubenfels, 1930	EPac, Mex, Calif	2
Membranobalanus	longirostrum (Hoek, 1913)	Hadromerida	Clionidae	Sphectospongia	purpurea (Lamarck, 1814); inconspans (Dendy, 1887)	India; Singapore	2
Pygospingia	sp. 1	Hadromerida	Clionidae	Sphectospongia	vagabunda (Ridley, 1884)	Malaysia	QM G304993
Membranobalanus	declivis (Darwin, 1854)	Hadromerida	Clionidae	Sphectospongia	vesparium (Lamarck, 1815)	Caribbean, WAtl	CASIZ 166611
Acacia	sp. 35	Hadromerida	Hemiasterellidae	Hemiasterella		WA	QM G300208
Archiacacia	pustulata Kolbasov, 1993	Hadromerida	Spirastrellidae	Spirastrella		Indian Ocean	1
Acacia	sp. L	Hadromerida	Suberitidae	Aaptos	suberitoides (Bromsted, 1934)	Philippines	CASIZ 179566, ZMAPOR 21935
Acacia	sp. 84	Hadromerida	Suberitidae	Protosuberites	sp. 1	QLD	RVS469A
Neocasta	scuticosta (Welter, 1887)	Hadromerida	Tethyidae	Tethya	aurantium (Pallas, 1766)	Spain	Orig. descr.
Acacia	sp. 86	Hadromerida	Tethyidae	Tethya		WA	QM G306033
Neocasta	glans (Lamarck, 1818)	Halichondrida	Axinellidae	Axinella		Indian Ocean	1
Acacia	sp. 10	Halichondrida	Axinellidae	Cymbastela	canharella (Lévi, 1983)	New Caledonia	QM G300015
Acacia	sp. 11	Halichondrida	Axinellidae	Cymbastela	concentrica (Lendenfeld, 1887)	QLD	QM G301234
Acacia	sp. 11	Halichondrida	Axinellidae	Cymbastela	concentrica (Lendenfeld, 1887)	New Caledonia	QM G301229
Acacia	sp. 11	Halichondrida	Axinellidae	Cymbastela	concentrica (Lendenfeld, 1887)	New Caledonia	QM G301230
Acacia	sp. 11	Halichondrida	Axinellidae	Cymbastela	concentrica (Lendenfeld, 1887)	New Caledonia	QM G301266
Acacia	sp. 11	Halichondrida	Axinellidae	Cymbastela	concentrica (Lendenfeld, 1887)	New Caledonia	QM G301268
Acacia	sp. 12	Halichondrida	Axinellidae	Cymbastela	concentrica (Lendenfeld, 1887)	QLD	QM G301233
Acacia	sp. 14	Halichondrida	Axinellidae	Cymbastela	concentrica (Lendenfeld, 1887)	QLD	QM G317482
Acacia	sp. 14	Halichondrida	Axinellidae	Cymbastela	coralliophila Hooper & Bergquist, 1992	QLD	QM G301232

TABLE 1 (continued). Sponge-inhabiting barnacles, their host sponges and references for host identifications. Sorted by sponge taxon. References are designated as Original Description, QMP, ZAMPOR, or CASIZ catalog numbers, or RVS field numbers, 1 = Kolbasov, 1993, 2 = Van Syoc & Winther, 1999, 3 = Ilan et al., 1999, 4 = Van Syoc & Newman, 2010.

Barnacle Genus	Barnacle Species	Sponge Order	Sponge Family	Sponge Genus	Sponge Species	Locality	Reference
Acasta	sp. 14	Halichondrida	Axinellidae	Cymbastela	coralliophila Hooper & Bergquist, 1992	QLD	QM G314309
Acasta	sp. 14	Halichondrida	Axinellidae	Cymbastela	coralliophila Hooper & Bergquist, 1992	QLD	QM G303911
Acasta	sp. 11	Halichondrida	Axinellidae	Cymbastela	marshae Hooper & Bergquist, 1992	WA	QM G300005
Acasta	sp. 16	Halichondrida	Axinellidae	Cymbastela	notiata Hooper & Bergquist, 1992	SA	QM G301231
Acasta	sp. 91	Halichondrida	Axinellidae	Cymbastela	coralliophila Hooper & Bergquist, 1992	QLD	QM G303855
Acasta	sp. 91	Halichondrida	Axinellidae	Cymbastela	coralliophila Hooper & Bergquist, 1992	QLD	QM G303016
Acasta	sp. F	Halichondrida	Axinellidae	Cymbastela	coralliophila Hooper & Bergquist, 1992	QLD	QM G300012
Acasta	sp. 19	Halichondrida	Axinellidae	Dragnacidom	australe (Bergquist, 1970)	Fiji	QM G312767
Acasta	sp. 20	Halichondrida	Axinellidae	Dragnacidom	debitusae (Hooper & Lévi, 1993)	New Caledonia	QM G301319
Acasta	sp. 20	Halichondrida	Axinellidae	Dragnacidom	debitusae (Hooper & Lévi, 1993)	New Caledonia	QM G301332
Acasta	paraspiniifera Kim & Kim, 1988	Halichondrida	Axinellidae	Phakellia	elegans Thiele, 1898	S. Korea	Orig. descr.
Archiacasta	spiniifera (Utinomi, 1967)	Halichondrida	Axinellidae	Phakellia		Japan	1
Acasta	sp. 17	Halichondrida	Axinellidae	Phycopsis		WA	QM G300223
Acasta	rimiformis Kolbasov, 1991	Halichondrida	Axinellidae	unknown		Indian Ocean	1
Acasta	tzetlini Kolbasov, 1992	Halichondrida	Axinellidae	unknown		Indian Ocean	1
Eucasta	"dofleinii" (Kruger, 1911)	Halichondrida	Axinellidae	unknown		Indian Ocean	1
Acasta	sp. 18	Halichondrida	Dicyonellidae	Stylissa	cauteri (Dendy, 1889)	WA	QM G301138
Acasta	sp. 17	Halichondrida	Dicyonellidae	Stylissa		Thailand	QM G300251
Acasta	sp. 21	Halichondrida	Dicyonellidae	Stylissa		Thailand	QM G300250
Acasta	sp. 33	Halichondrida	Halichondriidae	Epipolasis		QLD	QM G305527
Acasta	sp. 18	Halichondrida	Halichondriidae	Halichondria		NT	QM G300175
Acasta	sp. 34	Halichondrida	Halichondriidae	Halichondria		QLD	QM G305465
Acasta	sp. 5	Halichondrida	Halichondriidae	Halichondria		WA	QM G306054
Acasta	aperta (Hiro, 1931)	Halichondrida	Halichondriidae	Halichondria (Halichondria)	okadai, japonica (Kadota, 1922)	Japan	Orig. descr.
Acasta	komaii Hiro, 1931	Halichondrida	Halichondriidae	Halichondria (Halichondria)	okadai, japonica (Kadota, 1922)	Japan	Orig. descr.
Neocasta	glans (Lamarck, 1818)	Halichondrida	Halichondriidae	unknown		Indian Ocean	1
Pectinoacasta	pectinipes (Pilsbry, 1912)	Halichondrida	Halichondriidae	unknown		Indian Ocean	1
Acasta	sp. 31	Halichondrida	Heteroxyidae	Myrmekioderma	granulatum (Esper, 1794)	WA	QM G301141
Acasta	sp. 32	Halichondrida	Heteroxyidae	Myrmekioderma	granulatum (Esper, 1794)	QLD	QM G304866
Acasta	sp. 22	Haplosclerida	Callyspongiidae	Callyspongia		QLD	QM G303889
Acasta	sp. 23	Haplosclerida	Callyspongiidae	Callyspongia		QLD	QM G305439
Acasta	sp. 25	Haplosclerida	Callyspongiidae	Callyspongia (Euplaccella)		QLD	QM G305438
Acasta	sp. 25	Haplosclerida	Callyspongiidae	Callyspongia (Euplaccella)		QLD	QM G305565
Acasta	sp. 24	Haplosclerida	Chalimidae	Dactylia		QLD	RVS467A
Acasta	"cyathus" Darwin, 1854	Haplosclerida	Chalimidae	Haliciona		Indian Ocean	1
Acasta	daedalusa Kolbasov, 1993	Haplosclerida	Chalimidae	Haliciona		Indian Ocean	1
Acasta	fenestrata Darwin, 1854	Haplosclerida	Chalimidae	Haliciona		Indian Ocean	1

TABLE 1 (continued). Sponge-inhabiting barnacles, their host sponges and references for host identifications. Sorted by sponge taxon. References are designated as Original Description, QMP, ZAMPOR, or CASIZ catalog numbers, or RVS field numbers, 1 = Kolbasov, 1993, 2 = Van Syoc & Winther, 1999, 3 = Ilan et al., 1999, 4 = Van Syoc & Newman, 2010.

Barnacle Genus	Barnacle Species	Sponge Order	Sponge Family	Sponge Genus	Sponge Species	Locality	Reference
Acasta	sp. 26	Haplosclerida	Chalinidae	Haliclona		Malaysia	QM G300067
Acasta	sp. 26	Haplosclerida	Chalinidae	Haliclona		QLD	QM G305758
Acasta	sp. 26	Haplosclerida	Chalinidae	Haliclona		QLD	QM G305595
Acasta	sp. 27	Haplosclerida	Chalinidae	Haliclona		QLD	QM G303912
Acasta	sulcata Lamarck, 1818	Haplosclerida	Chalinidae	Haliclona		Indian Ocean	1
Archiacasta	tenuivalvata Broch, 1947	Haplosclerida	Chalinidae	Haliclona		Indian Ocean	1
Euacasta	"dofleini" (Krugger, 1911)	Haplosclerida	Chalinidae	Haliclona		Indian Ocean	1
Euacasta	porata(Nielsen-Cantell, 1921)	Haplosclerida	Chalinidae	Haliclona		Indian Ocean	1
Pectinoacasta	zevinae (Kolbasov, 1991)	Haplosclerida	Chalinidae	Haliclona		PNG	1
Euacasta	"dofleini" (Krugger, 1911)	Haplosclerida	Chalinidae	Haliclona (Gellius)		Indian Ocean	1
Acasta	armata Gravier, 1921	Haplosclerida	Chalinidae	unknown		Djibouti	Orig. descr.
Acasta	perusa Kolbasov, 1990b	Haplosclerida	Chalinidae	unknown		Red Sea	1
Neoacasta	planibasis Kolbasov, 1993	Haplosclerida	Chalinidae	unknown		Indian Ocean	1
Acasta	sp. 51	Haplosclerida	Niphathiidae	Amphimedon		NT	QM G301199
Acasta	sp. 54	Haplosclerida	Niphathiidae	Niphates		Singapore	QM G304040
Acasta	sp. 55	Haplosclerida	Niphathiidae	Niphates		QLD	QM G306216
Acasta	sp. 55	Haplosclerida	Niphathiidae	Niphates		QLD	QM G306217
Acasta	sp. 52	Haplosclerida	Niphathiidae	Pipestela	terpenensis (Fromont, 1993)	QLD	QM G303001
Acasta	sp. 53	Haplosclerida	Niphathiidae	Pipestela	terpenensis (Fromont, 1993)	QLD	QM G305393
Acasta	sp. M	Haplosclerida	Petrosiidae	Acanthostromylophora	ingens (Thiel, 1899)	Philippines	CASIZ 179564, ZMAPOR
Acasta	sp. G	Haplosclerida	Petrosiidae	Neopetrosia	exigua (Kirkpatrick, 1900)	QLD	QM G320490
Acasta	sp. H	Haplosclerida	Petrosiidae	Neopetrosia	exigua (Kirkpatrick, 1900)	Philippines	CASIZ 180280, ZMAPOR
Acasta	sp. H	Haplosclerida	Petrosiidae	Neopetrosia	exigua (Kirkpatrick, 1900)	Philippines	CASIZ 180281, ZMAPOR
Acasta	sp. H	Haplosclerida	Petrosiidae	Petrosia		Indian Ocean	1
Acasta	sp. H	Haplosclerida	Petrosiidae	Petrosia		Fiji	QM G312858
Acasta	sp. H	Haplosclerida	Petrosiidae	Petrosia		Indian Ocean	Orig. descr.
Acasta	sp. 57	Haplosclerida	Petrosiidae	Petrosia		WA	QM G301080
Euacasta	abnormis (Kolbasov, 1991)	Haplosclerida	Petrosiidae	Petrosia		Indian Ocean	1
Acasta	sp. 57	Haplosclerida	Petrosiidae	Xestospongia	testudinaria (Lamarck, 1815)	WA	QM G306055
Acasta	sp. 58	Haplosclerida	Petrosiidae	Xestospongia		QLD	QM G305063
Acasta	sp. 60	Haplosclerida	Phloeodictyidae	Oceanapia	ramsayi (Lendenfeld, 1888)	WA	QM G306052
Acasta	sp. 59	Haplosclerida	Phloeodictyidae	Oceanapia		QLD	QM G305656
Acasta	sp. 74	Lithisida	Scleritodermidae	Scleritodermia		WA	QM G306193
Euacasta	tabachnicki (Kolbasov, 1990a)	Lyssacinosida	Euplectellidae	Euplectella	aspergillum Owen, 1841	Indian Ocean	1
Acasta	sp. 50	Poecilosclerida	Chondropsidae	Photospingia		QLD	QM G304010
Acasta	sp. 50	Poecilosclerida	Chondropsidae	Photospingia		QLD	QM G303980
Acasta	sp. 70	Poecilosclerida	Chondropsidae	Photospingia		QLD	QM G305397

TABLE 1 (continued). Sponge-inhabiting barnacles, their host sponges and references for host identifications. Sorted by sponge taxon. References are designated as Original Description, QMP, ZMAPOR, or CASIZ catalog numbers, or RVS field numbers, 1 = Kolbasov, 1993, 2 = Van Syoc & Winther, 1999, 3 = Ilan et al., 1999, 4 = Van Syoc & Newman, 2010.

Barnacle Genus	Barnacle Species	Sponge Order	Sponge Family	Sponge Genus	Sponge Species	Locality	Reference
Acasta	koltuni Kolbasov, 1991	Poecilosclerida	Coelospaeridae	Coelospaera		Indian Ocean	1
Multatira	sp. 2	Poecilosclerida	Crambeidae	Monanchora	laevissima (Dendy, 1922)	Madagascar	4
Multatira	sp. 1	Poecilosclerida	Crambeidae	Monanchora	unguiculata (Dendy, 1922)	Palau	4
Acasta	infirmia Kolbasov, 1992	Poecilosclerida	Crellidae	Crella		Indian Ocean	1
Eucasta	"dofleini" (Kruger, 1911)	Poecilosclerida	Crellidae	Crella		Indian Ocean	1
Acasta	sp. 28	Poecilosclerida	Crellidae	Crella (Yvesia)	spinulata (Hentschel, 1911)	WA	QM G300221
Acasta	sp. 29	Poecilosclerida	Crellidae	Crella (Yvesia)	spinulata (Hentschel, 1911)	NT	QM G301206
Acasta	sp. 30	Poecilosclerida	Desmaccellidae	Ncofibularia	irata Wilkinson, 1978	QLD	QM G305679
Eucasta	"dofleini" (Kruger, 1911)	Poecilosclerida	Desmaccellidae	Desmaccidon		WA	QM G306144
Acasta	sp. 40	Poecilosclerida	Desmaccellidae	unknown		Red Sea	1
Acasta	sp. 41	Poecilosclerida	Microcionidae	Antho (Acanthia)	ridleyi (Hentschel, 1912)	NT	QM G300146
Acasta	sp. 40	Poecilosclerida	Microcionidae	Clathria (Clathria)	conectens (Hallmann, 1912)	QLD	QM G304888
Eoatria	sp. 1	Poecilosclerida	Microcionidae	Clathria (Clathria)	conectens (Hallmann, 1912)	QLD	QM G304980
Eoatria	sp. 4	Poecilosclerida	Microcionidae	Clathria (Clathria)	kylista Hooper & Lévi, 1993	QLD	QM G305498
Bryozobia	synaptos Ross & Newman, 1996	Poecilosclerida	Microcionidae	Clathria (Microciona)		Madagascar	4
Eoatria	sp. 2	Poecilosclerida	Microcionidae	Clathria (Microciona)		QLD	QM G305768
Eoatria	sp. 3	Poecilosclerida	Microcionidae	Clathria (Microciona)		QLD	QM G305450
Microporatria	loreleyae Van Syoc & Newman, 2010	Poecilosclerida	Microcionidae	Clathria (Microciona)		Solomon Is.	4
Acasta	sp. 44	Poecilosclerida	Microcionidae	Clathria (Thalysias)	abietina (Lamarck, 1814)	WA	QM G306154
Acasta	sp. K	Poecilosclerida	Microcionidae	Clathria (Thalysias)	aff. eratica (Esper, 1797)	Philippines	CASIZ 179563, ZMAPOR 21932
Acasta	sp. 45	Poecilosclerida	Microcionidae	Clathria (Thalysias)	hirsuta Hooper & Lévi, 1993	New Caledonia	QM G301274
Acasta	sp. 46	Poecilosclerida	Microcionidae	Clathria (Thalysias)	hirsuta Hooper & Lévi, 1993	QLD	QM G303971
Acasta	sp. 47	Poecilosclerida	Microcionidae	Clathria (Thalysias)	lendenfeldi Ridley & Dendy, 1886	QLD	QM G303025
Acasta	sp. I	Poecilosclerida	Microcionidae	Clathria (Thalysias)	reinwardti Vosmaer, 1880	Philippines	CASIZ 179522, ZMAPOR 21751
Eoatria	goshneri Van Syoc & Newman, 2010	Poecilosclerida	Microcionidae	Clathria (Thalysias)	tingens Hooper, 1996	Palau	4
Acasta	sp. 48	Poecilosclerida	Microcionidae	Clathria (Wilsonella)	australiensis Carter, 1885	WA	QM G300133
Acasta	sp. 50	Poecilosclerida	Microcionidae	Echinochalina (Echinochalina)	intermedia (Whitelegge, 1902)	QLD	QM G304883
Acasta	sulcata Lamarck, 1818	Poecilosclerida	Myxillidae	unknown		Indian Ocean	1
Eucasta	"dofleini" (Kruger, 1911)	Poecilosclerida	Myxillidae	unknown		PNG	1
Acasta	sp. 39	Poecilosclerida	Podospongiidae	Diacarnus	spinopoculum (Carter, 1879)	QLD	QM G305467
Acasta	sp. 39	Poecilosclerida	Podospongiidae	Diacarnus	spinopoculum (Carter, 1879)	Fiji	QM G312833
Acasta	chejudoensis Kim & Kim, 1988	Poecilosclerida	Podospongiidae	Ceratopson		S. Korea	Orig. descr.
Acasta	sp. J	Poecilosclerida	Raspaillidae	Echinodicyum	flabelliforme (Keller, 1889)	Philippines	CASIZ 179521, ZMAPOR 21750
Acasta	sp. N	Poecilosclerida	Raspaillidae	Ectyoplasia	vannus Hooper, 1991	NT	QM G303651
Acasta	sp. 73	Poecilosclerida	Raspaillidae	Raspailla (Parasyringella)	muda Hentschel, 1911	NT	QM G300160
Acasta	sp. 72	Poecilosclerida	Raspaillidae	Raspailla (Parasyringella)		PNG	QM G312933
Acasta	sp. 71	Poecilosclerida	Raspaillidae	Raspailla (Raspaxilla)		QLD	QM G306292

TABLE 1 (continued). Sponge-inhabiting barnacles, their host sponges and references for host identifications. Sorted by sponge taxon. References are designated as Original Description, QMP, ZAMPOR, or CASIZ catalog numbers, or RVS field numbers, 1 = Kolbasov, 1993, 2 = Van Syoc & Winther, 1999, 3 = Ilan et al., 1999, 4 = Van Syoc & Newman, 2010.

Barnacle Genus	Barnacle Species	Sponge Order	Sponge Family	Sponge Genus	Sponge Species	Locality	Reference
Acasta	sp. 85	Poecilosclerida	Tetaniidae	Tetania		QLD	QM G301045
Acasta	sp. 88	Spirophorida	Tetillidae	Cinaehyrella	australiensis (Carter, 1886)	QLD	QM G304096
Acasta	sp. 89	Spirophorida	Tetillidae	Cinaehyrella	schulzei (Keller, 1891)	QLD	QM G304889
Acasta	sp. 87	Spirophorida	Tetillidae	Cinaehyrella		NT	QM G303633
Acasta	sp. 90	Verongida	Aplysiniidae	Aplysiniopsis	reticulata Lendenfeld, 1889	WA	QM G301164
Acasta	sp. 90	Verongida	Aplysiniidae	Aplysiniopsis	reticulata Lendenfeld, 1889	WA	QM G301182
Acasta	alba Barnard, 1924	unknown	unknown	unknown		Southern Africa	Orig. descr.
Acasta	amakusana (Hiro, 1931)	unknown	unknown	unknown		Japan	Orig. descr.
Acasta	apertura (Rosell, 1991)	unknown	unknown	unknown		Philippines	Orig. descr.
Acasta	conica Hoek, 1913	unknown	unknown	unknown		Indonesia	Orig. descr.
Acasta	coriolis Rosell, 1991	unknown	unknown	unknown		Philippines	Orig. descr.
Acasta	denticulata (Hiro, 1931)	unknown	unknown	unknown		Japan	Orig. descr.
Acasta	foraminifera Broch, 1931	unknown	unknown	unknown		Java Sea	Orig. descr.
Acasta	idlopoma Pilsbry, 1912	unknown	unknown	unknown		Philippines	Orig. descr.
Acasta	japonica Pilsbry, 1911	unknown	unknown	unknown		Japan	Orig. descr.
Acasta	madagascariensis Ren, 1989	unknown	unknown	unknown		Madagascar	Orig. descr.
Acasta	semota Hiro, 1933	unknown	unknown	unknown		Japan	Orig. descr.
Acasta	serrata Hiro, 1937	unknown	unknown	unknown		Palau	Orig. descr.
Acasta	spinosa Hiro, 1939	unknown	unknown	unknown		Taiwan	Orig. descr.
Acasta	striata Gruvel, 1901	unknown	unknown	unknown		Madeira	Orig. descr.
Archiacasta	praerupta (Foster, 1981)	unknown	unknown	unknown		New Zealand	Orig. descr.
Archiacasta	tulipa (Hiro, 1933)	unknown	unknown	unknown		Japan	Orig. descr.
Euacasta	aculeata (Nilsson-Cantell, 1921)	unknown	unknown	unknown		Thailand	Orig. descr.
Euacasta	ctenodentia (Rosell, 1972)	unknown	unknown	unknown		Philippines	Orig. descr.
Euacasta	zuiho (Hiro, 1936)	unknown	unknown	unknown		NT	Orig. descr.
Membranobalanus	orcuffiformis (Kolosváry, 1941)	unknown	unknown	unknown		Indian Ocean	Orig. descr.
Neocasta	coriobasis (Broch, 1947)	unknown	unknown	unknown		S. China Sea	Orig. descr.
Neocasta	fossata (Barnard, 1924)	unknown	unknown	unknown		Southern Africa	Orig. descr.
Pectinoacasta	angusticalcar (Broch, 1931)	unknown	unknown	unknown		Indonesia	Orig. descr.
Pectinoacasta	cancellorum (Hiro, 1931)	unknown	unknown	unknown		Japan	Orig. descr.
Pectinoacasta	sculpturata (Broch, 1931)	unknown	unknown	unknown		Java Sea	Orig. descr.
Poratria	williamsi Van Syoc & Newman, 2010	unknown	unknown	unknown		PNG	4
Euacasta	dofleini (Kruger, 1911)	various	various	various		IWP, Red Sea	1

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Barnacle Genus	Barnacle Species	Sponge Order	Sponge Family	Sponge Genus	Sponge Species	Locality	Reference
Acasta	acuta (Kolbasov, 1993)	Haplosclerida	Petrosiidae	Neopetrosia	exigua (Kirkpatrick, 1900)	QLD	QM G320490
Acasta	acuta (Kolbasov, 1993)	Haplosclerida	Petrosiidae	Petrosia		Indian Ocean	1
Acasta	acuta (Kolbasov, 1993)	Haplosclerida	Petrosiidae	Petrosia		Fiji	QM G312858
Acasta	alba Barnard, 1924	unknown	unknown	unknown		Southern Africa	Orig. descr.
Acasta	amakusana (Hiro, 1931)	unknown	unknown	unknown		Japan	Orig. descr.
Acasta	aperta (Hiro, 1931)	Halichondrida	Halichondriidae	Halichondria (Halichondria)	okadai, japonica (Kadota, 1922)	Japan	Orig. descr.
Acasta	apertura (Rosell, 1991)	unknown	unknown	unknown		Philippines	Orig. descr.
Acasta	armata Gravier, 1921	Haplosclerida	Chalinidae	unknown		Djibouti	Orig. descr.
Acasta	chejuensis Kim & Kim, 1988	Poecilosclerida	Raspatiliidae	Ceratopston		S. Korea	Orig. descr.
Acasta	collucata Kolbasov, 1992	Dictyoceratida	Spongiidae	Spongia		Indian Ocean	Orig. descr.
Acasta	conica Hoek, 1913	unknown	unknown	unknown		Indonesia	Orig. descr.
Acasta	coriolis Rosell, 1991	unknown	unknown	unknown		Philippines	Orig. descr.
Acasta	crassa Broch, 1931	Agelasida	Agelasidae	Agelas		Indonesia	1
Acasta	cyathus Darwin, 1854	Dictyoceratida	Spongiidae	Spongia (Spongia)	tubulifera Lamarck, 1814	Caribbean, WA II	2
Acasta	"cyathus" Darwin, 1854	Astrophorida	Ancorinidae	unknown		Indian Ocean	1
Acasta	"cyathus" Darwin, 1854	Dictyoceratida	Dysideidae	Dysidea		Indian Ocean	1
Acasta	"cyathus" Darwin, 1854	Haplosclerida	Chalinidae	Haliclona		Indian Ocean	1
Acasta	"cyathus" Darwin, 1854	unknown	Thorectidae	Hyrtios	erectus (Keller, 1889)	Red Sea	3
Acasta	daedalusa Kolbasov, 1993	Haplosclerida	Chalinidae	Haliclona		Indian Ocean	1
Acasta	denticulata (Hiro, 1931)	unknown	unknown	unknown		Japan	Orig. descr.
Acasta	fenestrata Darwin, 1854	Haplosclerida	Chalinidae	Haliclona		Indian Ocean	1
Acasta	fleuxosa Nilsson-Cantell, 1931	Dictyoceratida	Dysideidae	Dysidea		Indian Ocean	1
Acasta	foraminifera Broch, 1931	unknown	unknown	unknown		Java Sea	Orig. descr.
Acasta	idiopoma Pilsbry, 1912	unknown	unknown	unknown		Philippines	Orig. descr.
Acasta	infrima Kolbasov, 1992	Poecilosclerida	Crellidae	Crella		Indian Ocean	1
Acasta	japonica Pilsbry, 1911	unknown	unknown	unknown		Japan	Orig. descr.
Acasta	koltuni Kolbasov, 1991	Poecilosclerida	Coelospaeridae	Coelospaera		Indian Ocean	1
Acasta	komaii Hiro, 1931	Halichondrida	Halichondriidae	Halichondria (Halichondria)	okadai, japonica (Kadota, 1922)	Japan	Orig. descr.
Acasta	madagascariensis Ren, 1989	unknown	unknown	unknown		Madagascar	Orig. descr.
Acasta	newmani Van Syoc & Winther, 1999	Astrophorida	Vulcanellidae	Pocillastra	temulaminaris (Sollas, 1886)	EPac, Mexico	2
Acasta	paraspiniifera Kim & Kim, 1988	Halichondrida	Axinellidae	Phakellia	elegans Thiele, 1898	S. Korea	Orig. descr.
Acasta	pertusa Kolbasov, 1990b	Haplosclerida	Chalinidae	Diacarnus		Red Sea	1
Acasta	pertusa Kolbasov, 1990b	Poecilosclerida	Podospongiidae	unknown	erythraenus Kelly-Borges & Yacelet, 1995	Red Sea	3
Acasta	rimiformis Kolbasov, 1991	Halichondrida	Axinellidae	unknown		Indian Ocean	1
Acasta	semota Hiro, 1933	unknown	unknown	unknown		Japan	Orig. descr.
Acasta	serrata Hiro, 1937	unknown	unknown	unknown		Palau	Orig. descr.
Acasta	sinica Ren, 1984	Haplosclerida	Petrosiidae	Petrosia		S. China Sea	Orig. descr.
Acasta	sp. 1 Ilan, et al.	Poecilosclerida	Podospongiidae	Negombata	magnifica (Keller, 1889)	Red Sea	3

TABLE 2 (continued): Sponge-inhabiting barnacles, their host sponges and references for host identifications. Sorted by barnacle taxon. References are designated as Original Description, QMP, ZMAPOR, or CASIZ catalog numbers, or RVS field numbers, 1 = Kolbasov, 1993, 2 = Van Syoc & Winther, 1999, 3 = Ilan et al., 1999, 4 = Van Syoc & Newman, 2010.

Barnacle Genus	Barnacle Species	Sponge Order	Sponge Family	Sponge Genus	Sponge Species	Locality	Reference
Acasta	sp. 2 Ilan, et al.	Poecilosclerida	Acanthidae	Acanthus		Red Sea	3
Acasta	sp. 5	Halichondrida	Halichondridae	Halichondria		WA	QM G306054
Acasta	sp. 6	Agelasida	Agelasidae	Agelas	axifera Hentschel, 1911	WA	QM G300198
Acasta	sp. 6	Agelasida	Agelasidae	Agelas	mauritana (Carter, 1883)	QLD	QM G304021
Acasta	sp. 9	Astrophorida	Ancorinidae	Melophilus	globostellata (Carter, 1883)	WA	QM G306165
Acasta	sp. 9	Astrophorida	Ancorinidae	Rhabdastrella	globostellata (Carter, 1883)	QLD	QM G300041
Acasta	sp. 9	Astrophorida	Ancorinidae	Rhabdastrella	globostellata (Carter, 1883)	QLD	QM G304884
Acasta	sp. 9	Astrophorida	Ancorinidae	Rhabdastrella	globostellata (Carter, 1883)	NT	QM G303634
Acasta	sp. 10	Halichondrida	Axinellidae	Cymbastela	cantharella (Lévi, 1983)	New Caledonia	QM G300015
Acasta	sp. 11	Halichondrida	Axinellidae	Cymbastela	concentrica (Lendenfeld, 1887)	QLD	QM G301234
Acasta	sp. 11	Halichondrida	Axinellidae	Cymbastela	concentrica (Lendenfeld, 1887)	New Caledonia	QM G301229
Acasta	sp. 11	Halichondrida	Axinellidae	Cymbastela	concentrica (Lendenfeld, 1887)	New Caledonia	QM G301230
Acasta	sp. 11	Halichondrida	Axinellidae	Cymbastela	concentrica (Lendenfeld, 1887)	New Caledonia	QM G301266
Acasta	sp. 11	Halichondrida	Axinellidae	Cymbastela	concentrica (Lendenfeld, 1887)	New Caledonia	QM G301268
Acasta	sp. 11	Halichondrida	Axinellidae	Cymbastela	marshae Hooper & Bergquist, 1992	WA	QM G300005
Acasta	sp. 12	Halichondrida	Axinellidae	Cymbastela	concentrica (Lendenfeld, 1887)	QLD	QM G301233
Acasta	sp. 14	Halichondrida	Axinellidae	Cymbastela	concentrica (Lendenfeld, 1887)	QLD	QM G317482
Acasta	sp. 14	Halichondrida	Axinellidae	Cymbastela	corallophila Hooper & Bergquist, 1992	QLD	QM G301232
Acasta	sp. 14	Halichondrida	Axinellidae	Cymbastela	corallophila Hooper & Bergquist, 1992	QLD	QM G314309
Acasta	sp. 14	Halichondrida	Axinellidae	Cymbastela	corallophila Hooper & Bergquist, 1992	QLD	QM G303911
Acasta	sp. 16	Halichondrida	Axinellidae	Cymbastela	notaina Hooper & Bergquist, 1992	SA	QM G301231
Acasta	sp. 17	Halichondrida	Axinellidae	Phycopsis		WA	QM G300223
Acasta	sp. 17	Halichondrida	Dictyonellidae	Stylissa		Thailand	QM G300251
Acasta	sp. 18	Halichondrida	Dictyonellidae	Stylissa	carteri (Dendy, 1889)	WA	QM G301138
Acasta	sp. 18	Halichondrida	Halichondridae	Halichondria		NT	QM G300175
Acasta	sp. 19	Halichondrida	Axinellidae	Drumacidon	australe (Bergquist, 1970)	Fiji	QM G312767
Acasta	sp. 20	Halichondrida	Axinellidae	Drumacidon	debitusae (Hooper & Lévi, 1993)	New Caledonia	QM G301319
Acasta	sp. 20	Halichondrida	Axinellidae	Drumacidon	debitusae (Hooper & Lévi, 1993)	New Caledonia	QM G301332
Acasta	sp. 21	Halichondrida	Dictyonellidae	Stylissa		Thailand	QM G300250
Acasta	sp. 22	Haplosclerida	Callyspongiidae	Callyspongia		QLD	QM G303889
Acasta	sp. 23	Haplosclerida	Callyspongiidae	Callyspongia		QLD	QM G305439
Acasta	sp. 24	Haplosclerida	Callyspongiidae	Dactylia		QLD	RVS467A
Acasta	sp. 25	Haplosclerida	Callyspongiidae	Callyspongia (Euplaccella)		QLD	QM G305438
Acasta	sp. 25	Haplosclerida	Callyspongiidae	Callyspongia (Euplaccella)		QLD	QM G305565
Acasta	sp. 26	Haplosclerida	Chalmidae	Haliclona		Malaysia	QM G300067
Acasta	sp. 26	Haplosclerida	Chalmidae	Haliclona		QLD	QM G305758
Acasta	sp. 26	Haplosclerida	Chalmidae	Haliclona		QLD	QM G305595
Acasta	sp. 27	Haplosclerida	Chalmidae	Haliclona		QLD	QM G303912

TABLE 2 (continued): Sponge-inhabiting barnacles, their host sponges and references for host identifications. Sorted by barnacle taxon. References are designated as Original Description, QMP, ZMAPOR, or CASIZ catalog numbers, or RVS field numbers, 1 = Kolbasov, 1993, 2 = Van Syoc & Winther, 1999, 3 = Ilan et al., 1999, 4 = Van Syoc & Newman, 2010.

Barnacle Genus	Barnacle Species	Sponge Order	Sponge Family	Sponge Genus	Sponge Species	Locality	Reference
Acasta	sp. 28	Poecilosclerida	Crellidae	Crella (Yvesia)	spinulata (Hentschel, 1911)	WA	QM G300221
Acasta	sp. 28	Poecilosclerida	Crellidae	Crella (Yvesia)	spinulata (Hentschel, 1911)	NT	QM G301206
Acasta	sp. 29	Poecilosclerida	Desmaccellidae	Neofibularia	irata Wilkinson, 1978	QLD	QM G305679
Acasta	sp. 30	Poecilosclerida	Desmaccellidae	Desmaccidon		WA	QM G306144
Acasta	sp. 31	Halichondrida	Heteroxyidae	Myrmekioderma	granulatum (Esper, 1794)	WA	QM G301141
Acasta	sp. 32	Halichondrida	Heteroxyidae	Myrmekioderma	granulatum (Esper, 1794)	QLD	QM G304866
Acasta	sp. 33	Halichondrida	Halichondridae	Eppolasis		QLD	QM G305527
Acasta	sp. 34	Halichondrida	Halichondridae	Halichondria		QLD	QM G305465
Acasta	sp. 35	Hadromerida	Halichondridae	Halichondria		WA	QM G300208
Acasta	sp. 36	Dictyoecratida	Hemiassterellidae	Hemiassterella		QLD	QM G304116
Acasta	sp. 36	Dictyoecratida	Iremitidae	Iremita	bulbosa Bergquist, 1995	WA	QM G306050
Acasta	sp. 38	Dictyoecratida	Thorectidae	Thorecta		QLD	QM G300072
Acasta	sp. 39	Poecilosclerida	Podospongiidae	Diacamus	spinipoculum (Carter, 1879)	QLD	QM G305467
Acasta	sp. 39	Poecilosclerida	Podospongiidae	Diacamus	spinipoculum (Carter, 1879)	QLD	QM G312833
Acasta	sp. 40	Poecilosclerida	Microcionidae	Antho (Acanthia)	ridleyi (Hentschel, 1912)	Fiji	QM G300146
Acasta	sp. 41	Poecilosclerida	Microcionidae	Clathria (Clathria)	conectens (Hallmann, 1912)	NT	QM G304888
Acasta	sp. 44	Poecilosclerida	Microcionidae	Clathria (Thalysias)	abietina (Lamarck, 1814)	WA	QM G306154
Acasta	sp. 45	Poecilosclerida	Microcionidae	Clathria (Thalysias)	hirsuta Hooper & Lévi, 1993	New Caledonia	QM G301274
Acasta	sp. 46	Poecilosclerida	Microcionidae	Clathria (Thalysias)	hirsuta Hooper & Lévi, 1993	QLD	QM G303971
Acasta	sp. 47	Poecilosclerida	Microcionidae	Clathria (Thalysias)	lendenfeldi Ridley & Dendy, 1886	QLD	QM G303025
Acasta	sp. 48	Poecilosclerida	Microcionidae	Clathria (Wilsonella)	australensis Carter, 1885	WA	QM G300133
Acasta	sp. 50	Poecilosclerida	Chondropsidae	Phortospongia		QLD	QM G304010
Acasta	sp. 50	Poecilosclerida	Chondropsidae	Phortospongia		QLD	QM G303980
Acasta	sp. 50	Poecilosclerida	Microcionidae	Echinochalina (Echinochalina)	intermedia (Whitelegge, 1902)	QLD	QM G304883
Acasta	sp. 51	Haplosclerida	Niphatidae	Amphimedon		NT	QM G301199
Acasta	sp. 52	Haplosclerida	Niphatidae	Pipestela	terpenensis (Fromont, 1993)	QLD	QM G303001
Acasta	sp. 53	Haplosclerida	Niphatidae	Pipestela	terpenensis (Fromont, 1993)	QLD	QM G305393
Acasta	sp. 54	Haplosclerida	Niphatidae	Niphates		Singapore	QM G304040
Acasta	sp. 55	Haplosclerida	Niphatidae	Niphates		QLD	QM G306216
Acasta	sp. 55	Haplosclerida	Niphatidae	Niphates		QLD	QM G306217
Acasta	sp. 57	Haplosclerida	Petrosiidae	Petrosia	testudinaria (Lamarck, 1815)	WA	QM G301080
Acasta	sp. 57	Haplosclerida	Petrosiidae	Xestospongia		WA	QM G306055
Acasta	sp. 58	Haplosclerida	Petrosiidae	Xestospongia		QLD	QM G305063
Acasta	sp. 59	Haplosclerida	Phloeodictyidae	Oceania		QLD	QM G305656
Acasta	sp. 60	Haplosclerida	Phloeodictyidae	Oceania	ramsayi (Lendenfeld, 1888)	WA	QM G306052
Acasta	sp. 70	Poecilosclerida	Chondropsidae	Phortospongia		QLD	QM G305397
Acasta	sp. 71	Poecilosclerida	Raspailiidae	Raspailia (Raspaxilla)		QLD	QM G306292
Acasta	sp. 72	Poecilosclerida	Raspailiidae	Raspailia (Parasyringella)		PNG	QM G312933



TABLE 2 (continued): Sponge-inhabiting barnacles, their host sponges and references for host identifications. Sorted by barnacle taxon. References are designated as Original Description, QMP, ZMAPOR, or CASIZ catalog numbers, or RVS field numbers, 1 = Kolbasov, 1993, 2 = Van Syoc & Winther, 1999, 3 = Ilan et al., 1999, 4 = Van Syoc & Newman, 2010.

Barnacle Genus	Barnacle Species	Sponge Order	Sponge Family	Sponge Genus	Sponge Species	Locality	Reference
Acasta	sp. 73	Poecilosclerida	Raspaillidae	Raspailla (Parasyringella)	nuda Hentschel, 1911	NT	QM G300160
Acasta	sp. 74	Lithistida	Scleritodermidae	Scleritoderma		WA	QM G306193
Acasta	sp. 75	Dictyoceratida	Thorectidae	Carterospongia	flabellifera (Bowerbank, 1877)	QLD	QM G303017
Acasta	sp. 76	Dictyoceratida	Thorectidae	Carterospongia	flabellifera (Bowerbank, 1877)	QLD	QM G304114
Acasta	sp. 76 and 78	Agelasida	Agelasidae	Agelas	mauritiama (Carter, 1883)	QLD	QM G314522
Acasta	sp. 78	Dictyoceratida	Thorectidae	Carterospongia	flabellifera (Bowerbank, 1877)	QLD	QM G317495
Acasta	sp. 78	Dictyoceratida	Thorectidae	Carterospongia	cf. foliascens (Pallas, 1766)	WA	QM G306046
Acasta	sp. 78	Dictyoceratida	Thorectidae	Carterospongia	cf. foliascens (Pallas, 1766)	WA	QM G306164
Acasta	sp. 79	Dictyoceratida	Thorectidae	Dactylospongia		PNG	QM G312881
Acasta	sp. 80	Dictyoceratida	Spongiidae	Hippospongia	cf. communis (Lamarck, 1814)	QLD	QM G305064
Acasta	sp. 80	Dictyoceratida	Thorectidae	Lendenfeldia	plicata (Esper, 1794)	QLD	QM G304093
Acasta	sp. 80	Dictyoceratida	Thorectidae	Strepsichordia	lendenfeldi Bergquist, Ayling & Wilkinson, 1988	QLD	QM G303910
Acasta	sp. 81	Dictyoceratida	Thorectidae	Phyllospongia	lamellosa (Esper, 1794)	QLD	QM G305424
Acasta	sp. 81	Dictyoceratida	Thorectidae	Phyllospongia	papyracea (Esper, 1794)	QLD	QM G303018
Acasta	sp. 82	Dictyoceratida	Thorectidae	Phyllospongia	papyracea (Esper, 1794)	QLD	QM G317706
Acasta	sp. 83	Dictyoceratida	Spongiidae	Spongia		QLD	QM G303968
Acasta	sp. 84	Hadromerida	Suberitidae	Protosuberites	sp. 1	QLD	RVS469A
Acasta	sp. 85	Poecilosclerida	Tedaniidae	Tedania		QLD	QM G301045
Acasta	sp. 86	Hadromerida	Tethyidae	Tethya		WA	QM G306033
Acasta	sp. 87	Spirophorida	Tetillidae	Cinaachyrella		NT	QM G303633
Acasta	sp. 88	Spirophorida	Tetillidae	Cinaachyrella	australiensis (Carter, 1886)	QLD	QM G304096
Acasta	sp. 89	Spirophorida	Tetillidae	Cinaachyrella	schulzei (Keller, 1891)	QLD	QM G304889
Acasta	sp. 90	Verongida	Aplysiniidae	Aplysinopsis	reticulata Lendenfeld, 1889	WA	QM G301164
Acasta	sp. 90	Verongida	Aplysiniidae	Aplysinopsis	reticulata Lendenfeld, 1889	WA	QM G301182
Acasta	sp. 91	Halichondrida	Axinellidae	Cymbastella	corallophila Hooper & Bergquist, 1992	QLD	QM G303855
Acasta	sp. 91	Halichondrida	Axinellidae	Cymbastella	corallophila Hooper & Bergquist, 1992	QLD	QM G303016
Acasta	sp. A	Dictyoceratida	Dysideidae	Lamellodysidea	herbacea (Keller, 1889)	Philippines	CASIZ 179517, ZMAPOR 21746
Acasta	sp. B	Dictyoceratida	Thorectidae	Phyllospongia	papyracea (Esper, 1794)	Philippines	CASIZ 179519, ZMAPOR 21748
Acasta	sp. C	Dictyoceratida	Thorectidae	Phyllospongia	papyracea (Esper, 1794)	Philippines	CASIZ 179520, ZMAPOR 21749
Acasta	sp. D	Dictyoceratida	Thorectidae	Phyllospongia	papyracea (Esper, 1794)	MADAGASCAR	CASIZ 180562, ZMAPOR 21754
Acasta	sp. E	Dictyoceratida	Thorectidae	Strepsichordia	aff. lendenfeldi Bergquist, Ayling & Wilkinson, 1988	Philippines	CASIZ 179518, ZMAPOR 21747
Acasta	sp. F	Halichondrida	Axinellidae	Cymbastella	corallophila Hooper & Bergquist, 1992	QLD	QM G300012
Acasta	sp. G	Haplosclerida	Petrosiidae	Neopetrosia	exigua (Kirkpatrick, 1900)	Philippines	CASIZ 180280, ZMAPOR 21752
Acasta	sp. H	Haplosclerida	Petrosiidae	Neopetrosia	exigua (Kirkpatrick, 1900)	Philippines	CASIZ 180281, ZMAPOR 21753
Acasta	sp. I	Poecilosclerida	Microcionidae	Clathria (Thalysias)	reinwardti Vosmaer, 1880	Philippines	CASIZ 179522, ZMAPOR 21751
Acasta	sp. J	Poecilosclerida	Raspaillidae	Echinodictyum	flabelliforme (Keller, 1889)	Philippines	CASIZ 179521, ZMAPOR 21750
Acasta	sp. K	Poecilosclerida	Microcionidae	Clathria (Thalysias)	aff. cratita (Esper, 1797)	Philippines	CASIZ 179563, ZMAPOR 21932
Acasta	sp. L	Hadromerida	Suberitidae	Aaptos	suberitoides (Bronsted, 1934)	Philippines	CASIZ 179566, ZMAPOR 21935

TABLE 2 (continued): Sponge-inhabiting barnacles, their host sponges and references for host identifications. Sorted by barnacle taxon. References are designated as Original Description, QMP, ZMAPOR, or CASIZ catalog numbers, or RVS field numbers, 1 = Kolbasov, 1993, 2 = Van Syoc & Winther, 1999, 3 = Ilan et al., 1999, 4 = Van Syoc & Newman, 2010.

Barnacle Genus	Barnacle Species	Sponge Order	Sponge Family	Sponge Genus	Sponge Species	Locality	Reference
Acasta	sp. M	Haploclerida	Petrosiidae	Acanthostromylophora	ingens (Thiel, 1899)	Philippines	CASIZ 179564, ZMAPOR 21933
Acasta	sp. N	Poecilosclerida	Raspaillidae	Ectyoplasia	vannus Hooper, 1991	NT	QM G303651
Acasta	spinosa Hiro, 1939	unknown	unknown	unknown		Taiwan	Orig. descr.
Acasta	spongiformis Kolbasov, 1993	Astrophorida	Vulcanellidae	Pocillastrea		Indian Ocean	1
Acasta	spongites (Poli, 1791)	Dictyocerantida	Dysideidae	Dysidea		Indian Ocean	1
Acasta	striata Gruvel, 1901	unknown	unknown	unknown		Madeira	Orig. descr.
Acasta	sulcata Lamarck, 1818	Haploclerida	Chalinidae	Haliclona		Indian Ocean	1
Acasta	sulcata Lamarck, 1818	Poecilosclerida	Myxillidae	unknown		Indian Ocean	1
Acasta	tezlimi Kolbasov, 1992	Halichondrida	Aximellidae	Aximella	carteri (Dendy, 1889)	Madagascar, Red Sea	1, 3
Archiacasta	fragilis (Ren, 1984)	Dictyocerantida	Irciniidae	Ircinia		S. China Sea	Orig. descr.
Archiacasta	haianensis (Ren, 1984)	Dictyocerantida	Irciniidae	Ircinia		S. China Sea	Orig. descr.
Archiacasta	membranacea (Barnard, 1924)	Astrophorida	Pachastrellidae	Pachastrella	isorhopa Kirkpatrick, 1902	Southern Africa	Orig. descr.
Archiacasta	praenupta (Foster, 1981)	unknown	unknown	unknown		New Zealand	Orig. descr.
Archiacasta	pustulata Kolbasov, 1993	Hadromerida	Spirastrellidae	Spirastrella		Indian Ocean	1
Archiacasta	spinifera (Ujino, 1967)	Halichondrida	Aximellidae	Phakellia		Japan	1
Archiacasta	tenuivalvata Broch, 1947	Haploclerida	Chalinidae	Haliclona		Indian Ocean	1
Archiacasta	tulipa (Hiro, 1933)	unknown	unknown	unknown		Japan	Orig. descr.
Euacasta	abnormis (Kolbasov, 1991)	Haploclerida	Petrosiidae	Petrosia		Indian Ocean	1
Euacasta	aculeata (Nilsson-Cantell, 1921)	unknown	unknown	unknown		Thailand	Orig. descr.
Euacasta	ctenodentata (Rosell, 1972)	unknown	unknown	unknown		Philippines	Orig. descr.
Euacasta	dofleini (Kruger, 1911)	various	various	various		IWP, Red Sea	1
Euacasta	"dofleini" (Kruger, 1911)	Haploclerida	Chalinidae	Haliclona (Gellius)		Indian Ocean	1
Euacasta	"dofleini" (Kruger, 1911)	Haploclerida	Chalinidae	Haliclona		Indian Ocean	1
Euacasta	"dofleini" (Kruger, 1911)	Poecilosclerida	Myxillidae	unknown		PNG	1
Euacasta	"dofleini" (Kruger, 1911)	Halichondrida	Aximellidae	unknown		Indian Ocean	1
Euacasta	"dofleini" (Kruger, 1911)	Clathrinda	Leucetidae	Leucetta		Indian Ocean	1
Euacasta	"dofleini" (Kruger, 1911)	Poecilosclerida	Crellidae	Crella		Indian Ocean	1
Euacasta	"dofleini" (Kruger, 1911)	Astrophorida	Pachastrellidae	Pachastrella		Indian Ocean	1
Euacasta	"dofleini" (Kruger, 1911)	Poecilosclerida	Desmaaciidae	unknown		Red Sea	1
Euacasta	"dofleini" (Kruger, 1911)	"Lithistida"	Theonellidae	Theonella	conica (Kieschnick, 1896)	Red Sea	3
Euacasta	"dofleini" (Kruger, 1911)	Haploclerida	Callyspongiidae	Callyspongia		Red Sea	3
Euacasta	porata (Nilsson-Cantell, 1921)	Haploclerida	Chalinidae	Haliclona		Indian Ocean	1
Euacasta	sporillus (Darwin, 1854)	Dictyocerantida	Spongiidae	Spongia		Indian Ocean	1
Euacasta	tabachniki (Kolbasov, 1990a)	Lysacinosida	Euplectellidae	Euplectella	aspergillum Owen, 1841	Indian Ocean	1
Euacasta	zuiho (Hiro, 1936)	unknown	unknown	unknown		NT	Orig. descr.
Neocasta	coriobasis (Broch, 1947)	unknown	unknown	unknown		S. China Sea	Orig. descr.
Neocasta	fossata (Barnard, 1924)	unknown	unknown	unknown		Southern Africa	Orig. descr.
Neocasta	glans (Lamarck, 1818)	Halichondrida	Aximellidae	Aximella		Indian Ocean	1

TABLE 2 (continued): Sponge-inhabiting barnacles, their host sponges and references for host identifications. Sorted by barnacle taxon. References are designated as Original Description, QMP, ZMAPOR, or CASIZ catalog numbers, or RVS field numbers, 1 = Kolbasov, 1993, 2 = Van Syoc & Winther, 1999, 3 = Ilan et al., 1999, 4 = Van Syoc & Newman, 2010.

Barnacle Genus	Barnacle Species	Sponge Order	Sponge Family	Sponge Genus	Sponge Species	Locality	Reference
Neocasta	glans (Lamarck, 1818)	Halichondrida	Halichondriidae	unknown		Indian Ocean	1
Neocasta	laevigata (Gray, 1825)	Dietyoceratida	Dysideidae	Dysidea		Indian Ocean, PNG	1
Neocasta	laevigata (Gray, 1825)	Dietyoceratida	Spongiidae	unknown		Indian Ocean	1
Neocasta	laevigata (Gray, 1825)	Dietyoceratida	Spongiidae	Carteriospongia	foliascens	Red Sea	3
Neocasta	planibasis Kolbasov, 1993	Dietyoceratida	Dysideidae	Dysidea		Indian Ocean	1
Neocasta	planibasis Kolbasov, 1993	Haploclerida	Chalimidae	unknown		Indian Ocean	1
Neocasta	scuticosa (Welter, 1887)	Hadromerida	Tethyidae	Tethya	aurantium (Pallas, 1766)	Spain	Orig. deser.
Pectinoacasta	angusticalcar (Broch, 1931)	unknown	unknown	unknown		Indonesia	Orig. deser.
Pectinoacasta	cancellorum (Hiro, 1931)	unknown	unknown	unknown		Japan	Orig. deser.
Pectinoacasta	pectinipes (Pilsbry, 1912)	Halichondrida	Halichondriidae	unknown		Indian Ocean	1
Pectinoacasta	sculpturata (Broch, 1931)	unknown	unknown	unknown		Java Sea	Orig. deser.
Pectinoacasta	zevinae (Kolbasov, 1991)	Haploclerida	Chalimidae	Haliciona		PNG	1
Membranobalanus	brachialis (Rosell, 1972)	Hadromerida	Clonidae	Clona		Philippines	Orig. deser.
Membranobalanus	costatus Zullo & Standing, 1983	Hadromerida	Clonidae	Clona	varians Duchassaing & Michelotti, 1864	WAI, N Carolina	Orig. deser.
Membranobalanus	cuneiformis (Hiro, 1936)	Hadromerida	Clonidae	Clona		Japan	Orig. deser.
Membranobalanus	declivis (Darwin, 1854)	Hadromerida	Clonidae	Sphecospongia	vesparium (Lamarck, 1815)	Caribbean, WAI	CASIZ 166611
Membranobalanus	koreanus Kim & Kim, 1983	Hadromerida	Clonidae	Clona	aff. celtata Grant, 1826	S. Korea	Orig. deser.
Membranobalanus	longirostrum (Hoek, 1913)	Hadromerida	Clonidae	Sphecospongia	purpurea (Lamarck, 1814); inconstans (Dendy, 1887)	India; Singapore	2
Membranobalanus	longirostrum (Hoek, 1913)	Hadromerida	Suberitidae	Suberites	cf. clavatus Keller, 1891	Red Sea	3
Membranobalanus	nebriss (Zullo & Beach, 1973)	Hadromerida	Clonidae	Clona		Galapagos Is.	Orig. deser.
Membranobalanus	occuti (Pilsbry, 1907)	Hadromerida	Clonidae	Clona	aff. celtata Grant, 1826	EPac, Mex, Calif	2
Membranobalanus	occuti (Pilsbry, 1907)	Hadromerida	Clonidae	Sphecospongia	confederata de Laubentfels, 1930	EPac, Mex, Calif	2
Membranobalanus	occutiformis (Kolosváry, 1941)	unknown	unknown	unknown		Indian Ocean	Orig. deser.
Membranobalanus	robiniae Van Syoc, 1988	Hadromerida	Clonidae	Clona	raromicroclera (Dickinson, 1945)	EPac, Mexico	Orig. deser.
Membranobalanus	sp. 1	Hadromerida	Clonidae	Sphecospongia	areolata (Dendy, 1897)	NSW	QM G301439
Bryozobia	synaptos Ross & Newman, 1996	Poecilosclerida	Microcionidae	Clathria (Microciona)		Madagascar	4
Eoatria	gosimieri Van Syoc & Newman, 2010	Poecilosclerida	Microcionidae	Clathria (Thalysias)	tingens Hooper, 1996	Palau	4
Eoatria	sp. 1	Poecilosclerida	Microcionidae	Clathria (Clathria)	conectens (Hallmann, 1912)	QLD	QM G304980
Eoatria	sp. 2	Poecilosclerida	Microcionidae	Clathria (Microciona)		QLD	QM G305768
Eoatria	sp. 3	Poecilosclerida	Microcionidae	Clathria (Microciona)		QLD	QM G305450
Eoatria	sp. 4	Poecilosclerida	Microcionidae	Clathria (Clathria)		QLD	QM G305498
Microporatria	loreleyae Van Syoc & Newman, 2010	Poecilosclerida	Microcionidae	Clathria (Microciona)	kylista Hooper & Lévi, 1993	Solomon Is.	4
Mullatria	sp. 1	Poecilosclerida	Crambeidae	Monanchora	unguiculata (Dendy, 1922)	Palau	4
Mullatria	sp. 2	Poecilosclerida	Crambeidae	Monanchora	laevissima (Dendy, 1922)	Madagascar	4
Poratria	williamsi Van Syoc & Newman, 2010	unknown	unknown	unknown		PNG	4
Pyrgospongia	sp. 1	Hadromerida	Clonidae	Sphecospongia	vagabunda (Ridley, 1884)	Malaysia	QM G304993

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*Trachemys ornata* or not *ornata*:  
Reassessment of a Taxonomic Revision for Mexican *Trachemys*

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**The freshwater turtle genus *Trachemys* in Mexico has an unstable nomenclature with as few as one and as many as nine species (13 subspecies) currently considered valid by different groups of authors. The purpose of this study is to address a particular suggestion regarding the application of the principle of priority based on the finding that samples of *Trachemys ornata* Gray, 1830 are nested within *Trachemys venusta* 1856 in a molecular phylogeny. The previously sequenced samples of *T. "ornata"* are not from the main range and type region of *T. ornata* in Northwestern Mexico, but from a dubious, disjunct population in Acapulco, Guerrero. We show that *T. ornata* from the type region are not phylogenetically nested within *T. venusta* and that typical-looking *T. venusta* occur in the Acapulco region. Therefore, we conclude that the previous study did not sample true *T. ornata*. We recommend that *Trachemys* in the Atlantic drainages of Mexico and Central America should not be assigned to *T. ornata*, but rather remain in *T. venusta*.**

The freshwater turtle genus *Trachemys* Agassiz, 1857 in Mexico has an unstable nomenclature with as few as one and as many as nine species (13 subspecies) currently considered valid by different groups of authors (Seidel 2002; Jackson et al. 2008; McCord et al. 2010; Wiens et al. 2010; Fritz et al. 2012; Legler and Vogt 2013; McCranie et al. 2013; Parham et al. 2013; Forstner et al. 2014; Turtle Taxonomy Working Group 2014). Some of the disagreements about the number of lineages and the names they should bear stem from the application of different species concepts to limited data sets. Dense geographic sampling for morphological and molecular analyses is obviously necessary to establish a stable nomenclature for Mexican and Central American *Trachemys*. The purpose of this study is to address a particular suggestion regarding the application of the principle of priority based on samples of dubious identity.

In contrast to all recent workers, Fritz et al. (2012) recommended that almost all populations in Atlantic drainages of Mexico and Central America be changed from *Trachemys venusta* (Gray, 1856) to the older name *Trachemys ornata* (Gray, 1830) (a Pacific drainage species from Northwestern Mexico, Fig. 1). Their assertion is based on the finding that their samples of *T. ornata* are phylogenetically nested within *T. venusta*. However, their samples of *T. ornata* are not from the main range and type region of the species in Northwestern Mexico, but from a disjunct population

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in Acapulco, Guerrero, which has been considered uncertain by some authors (Legler 1990; Seidel 2002) and certain by others (Ernst 1990; Legler and Vogt 2013; Turtle Taxonomy Working Group, 2014). The dubious nature of these samples led Parham et al. (2013) to refrain from accepting this taxonomic suggestion to synonymize *T. venusta* with *T. ornata*.

The identity of *Trachemys* in the Acapulco region is central to the proposed taxonomic revision of Fritz et al. (2012). In this paper, we compare the genetics of *Trachemys* from the Acapulco region reported by Fritz et al. (2012) to those from *T. ornata* samples from the type region in Northwestern Mexico along with known locality samples of every named *Trachemys* from Mexico. We also provide new images and observations of turtles from the Acapulco region that, combined with the genetic data, and our interpretations, suggest that the recently proposed taxonomic revision was premature.



FIGURE 1. Map showing samples used in this study. Range maps are based on Legler and Vogt (2013) and the Turtle Taxonomy Working Group (2014) and should be considered approximate. Numbers correspond to samples analyzed for Fig. 2 and specimens in the Appendix. Specimens 35–38 are from beyond the southern limit of the map. Abbreviations: *T. n. h.* = *T. nebulosa hiltoni*; *T. s. e. x T. s. s.* = Intergrade zone for *T. s. elegans* and *T. s. scripta*

## MATERIALS AND METHODS

**NOMENCLATURE USED.**— As stated, the taxonomy of Mexican *Trachemys* is fluctuating. For the purpose of this study we largely adhere to the scheme of Parham et al. (2013), which is based on Seidel (2002). Parham et al. (2013) considered *Trachemys grayi* (Bocourt, 1868) a full species because it rendered *T. venusta* paraphyletic to *Trachemys emolli* (Legler, 1990). A genetic connection between *T. emolli* and *T. venusta* in Central America has been noted by Fritz et al. (2012) and Parham et al. (2013), with the former using this as evidence to place some populations of *T. venusta* into *T. grayi* and the latter indicating a potential hybrid zone between *T. emolli* and *T. venusta* in

need of further study. An additional departure from Seidel (2002) is the elevation of *Trachemys hartwegi* (Legler, 1990) to full species status following Forstner et al. (2014). *Trachemys hartwegi* was traditionally considered a morphologically distinct and allopatric subspecies of *T. gaigeae* (Hartweg, 1939) (Stuart and Ward 2009). Genetic data (Forstner et al. 2014; this study) show that it shares a recent common ancestry with *T. venusta*, and so continued recognition as a subspecies of *T. gaigeae* is untenable. Finally, following the argumentation of McCranie et al. (2013), we do not recognize the subspecies of *T. venusta* that were recently described in a European herpetological magazine (McCord et al. 2010).

**SAMPLES AND MARKER SELECTION.**— With the exception of sequences for four samples used from Fritz et al. (2012, one *Trachemys adiutrix* Vanzolini, 1995, one *Trachemys dorbigni* [Duméril and Bibron, 1835], and two putative *Trachemys ornata*), our study is based entirely on known-locality genetic samples with corresponding museum voucher specimens (Appendix). Fourteen samples were newly sequenced for this study (three *Trachemys hartwegi*, one *Trachemys nebulosa nebulosa* [Van Denburgh, 1895], four *Trachemys nebulosa hiltoni* [Carr, 1942], two *Trachemys ornata*, two *Trachemys taylori* [Legler, 1960], and two *Trachemys yaquia* [Legler and Webb, 1970]). The data for the remaining 21 samples (including the outgroup, not shown in Fig. 2) were taken from Parham et al. (2013). For all 39 samples, we analyze the mtDNA marker ('ND4,' see below) and nuclear marker (R35) that were used by both Parham et al. (2013) and Fritz et al. (2012). A summary of all samples including GenBank and voucher numbers can be found in the Appendix.

**EXTRACTIONS/PCR/SEQUENCING.**— Genomic DNA was extracted from approximately 25mg of liver tissue using the Qiagen DNeasy tissue kit (Qiagen, Valencia, CA) following manufacturer's instructions. A portion of the NADH dehydrogenase subunit 4 (ND4) gene, the complete tRNAs Histidine and Serine, and part of the tRNA Leucine ('ND4' hereafter) were amplified using primers L-ND4 and H-Leu (Stuart and Parham 2004). In addition, intron 1 of the fingerprint protein 35 (R35) was amplified using primers R35Ex1 and R35Ex2 (Fujita et al. 2004). For both the mitochondrial and nuclear markers, amplification reactions (25µl) contained ~50ng DNA, 1 X PCR buffer (20mM Tris-HCl, 50mM KCl), 1.5mM MgCl<sub>2</sub>, 0.4µM each primer, 200µM each dNTP and 1.25µ recombinant Taq DNA polymerase (Invitrogen). Thermal cycler profiles consisted of initial denaturation at 94°C for 2 min, followed by 35 cycles of 94°C for 30 s, 54–63°C for 30 s, and 72°C for 1–2 min, with a final extension at 72°C for 10 min. PCR products were then visualized on a 1% agarose gel and purified using ExoSAP-IT (USB, Cleveland Ohio). All samples were sequenced using the original PCR primers. Internal ND4 primers (L-ND4intEmys [TAGGCCTATGATGACTACTCG] and H-ND4intEmys [GAATGGCTATGTTGGCTAAGC]; primers designed by B.L. Stuart) and internal R35 primers (L-R35int and H-R35int; Stuart and Parham 2007) were used for sequencing. Sequences were assembled and edited using Geneious Pro 7.1.8 (Drummond et al. 2009). GenBank accession numbers for our new sequences and for sequences obtained from previous studies are provided (Appendix).

**ALIGNMENT AND PHYLOGENETIC ANALYSIS.**— The 'ND4' and R35 sequences used in the Fritz et al. (2012) and Parham et al. (2013) study were downloaded from Genbank (See Appendix for sample numbers, original citations for GenBank Accession numbers). All alignments were performed with MAFFT v7.017 (Katoh et al. 2002) followed by manual adjustments. The 'ND4' and R35 markers were concatenated and organized into biologically meaningful partitions; the R35 marker was treated as a single intron partition and the 'ND4' marker was partitioned by codon positions. Each partition was evaluated using the "from best-fit model" selected by AIC in MrModeltest 2.3 (Nylander 2004) via PAUP\*, version 4.0b10 (Swofford 2002). These models were assigned to the corresponding partitions for the Bayesian analyses performed in MrBayes MPI version 3.1.2

(Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003; Altekar et al. 2004). 10 million generations were run sampling every 1,000 trees with a “burnin” of 2,500 trees. Maximum likelihood (ML) analyses were performed in RAxML 7.2.6 (Stamatakis 2006). The GTR-Gamma model implemented in RAxML was used, which estimates and optimizes each partition for individual  $\alpha$ -shape parameters, GTR-rates, and empirical base frequencies. ML bootstrap analyses (10,000 replicates) employed the same model and search options as used in RAxML above.

RESULTS

We recover the same topology (Fig. 2) for *Trachemys* species groups found by other authors (Fritz et al. 2012, Parham et al. 2013): 1) Northern Clade including *T. scripta* and *T. gaigeae*; 2) West Indian Clade including Antillean taxa; 3) Southern Clade including taxa from internal and coastal drainages of Mexico, Central, and South America.

Within the Southern Clade there are five distinct subclades containing one or more species: 1) *T. nebulosa* with a long branch that could indicate a period of isolation on the Baja California Peninsula. Further sampling of *T. n. nebulosa* to compare with the mainland subspecies (*T. n. hiltoni*) is needed to test if the Baja California Peninsula is the area of origin for *T. nebulosa*; 2) South American taxa *T. aditrix* and *T. dorbigni*; 3) *T. emolli* and *T. grayi* from the Atlantic drainages of Southwestern Mexico and Central America; 4) Northwestern Mexico clade including *T. ornata* and *T. yaquia*; 5) *Trachemys venusta* clade including *T. taylori* and *T. hartwegi*. The species boundaries of these taxa and the relationship of *T. hartwegi* to *T. gaigeae* and *T. venusta* require further study. Samples from the Acapulco population of *T. “ornata”* are in this clade.

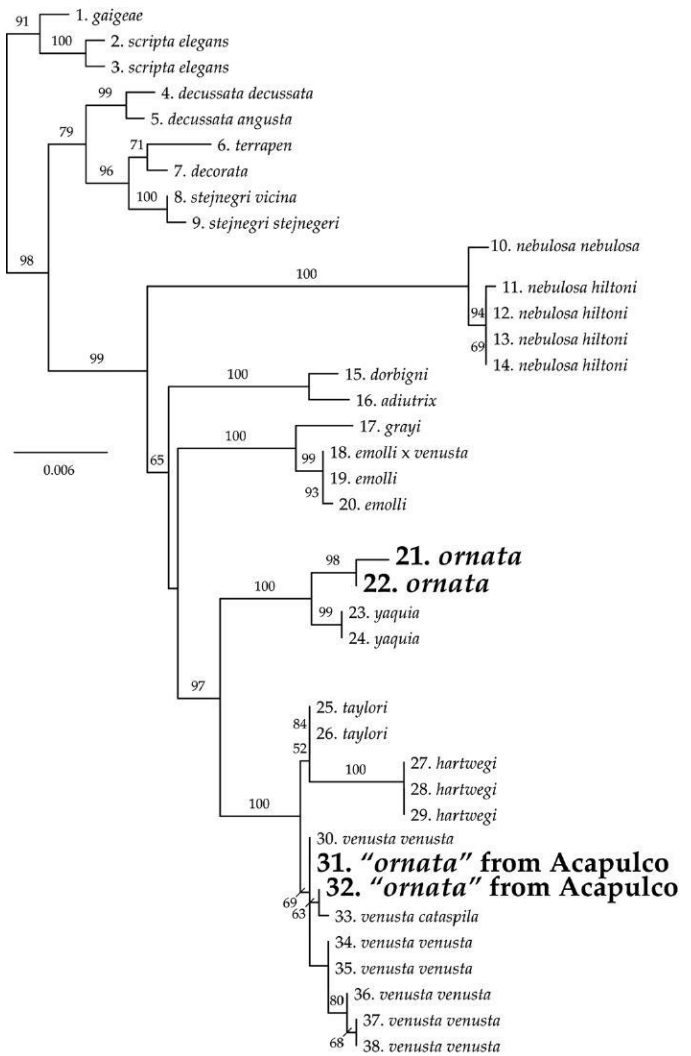


FIGURE 2. RaxML tree showing phylogenetic relationships of *Trachemys* samples including true *T. ornata* and the *T. “ornata”* from the disjunct population in the Acapulco region. Numbers correspond to localities in Fig. 1 and specimens in the Appendix. Scale bar represents number of substitutions per site.



## DISCUSSION

Our data show that *T. ornata* from the type region in the state of Sinaloa, in Northwestern Mexico, are not closely related to *T. venusta*, but rather to *T. yaquia*. This placement differs from that in Fritz et al. (2012), which analyzed samples from a putative disjunct population near Acapulco, Guerrero. The status of the Acapulco populations has been considered uncertain by some authors (Legler 1990; Seidel 2002) and certain by others (Ernst 1990; Legler and Vogt 2013; Turtle Taxonomy Working Group, 2014). We provide the first description of specimens from the Acapulco region, and show that they more closely match *T. venusta* in coloration. In July 2000, one of us (JRB) captured an adult and hatchling *Trachemys* in Tres Palos, Acapulco (Fig. 3). Both specimens differed from typical *T. ornata* by lacking discrete, centrally-located pleural ocelli (Fig. 4C), instead showing looping, loose, asymmetrical ocelli and streaks (Fig. 3) matching *T. venusta cataspila*. Also, unlike *T. ornata* from the type region, which have a green or blue iris (Fig. 4), individuals caught near Acapulco have a yellow iris (Fig. 3). In addition to the photographed individuals from Tres Palos, one of us (JRB) has seen wild turtles at Puerto Marques that also matched *T. venusta* more closely than *T. ornata*. This is significant because Puerto Marques is the origin of the samples used by Fritz et al. (2012).

The genetic data from Acapulco *Trachemys* combined with our observations suggest that the samples from the Fritz et al. (2012) study should be assigned to *T. venusta*, and do not represent *T. ornata*. We cannot confirm the identity of the samples used in Fritz et al. (2012) because there are no voucher specimens. Future research on the status and origin of the Acapulco *Trachemys* would be useful because it is possible that specimens of *T. ornata* also occur there, or that some individuals have mixed heritage. Because Acapulco is a resort area, it is also possible that specimens were moved to the area by tourists or as ornaments for water features.

Because the *T. "ornata"* samples from Fritz et al. (2012) represent *T. venusta*, they concluded that the two taxa should be synonymized, and because *T. ornata* is the older name, it would have priority. Our data show that *T. ornata* is not nested within *T. venusta*, and so we recommend that these two lineages should retain separate names. *Trachemys ornata* (type locality: Mazatlán, Sinaloa) is hereby restricted to populations in Northwest Mexico whereas *Trachemys venusta* (type

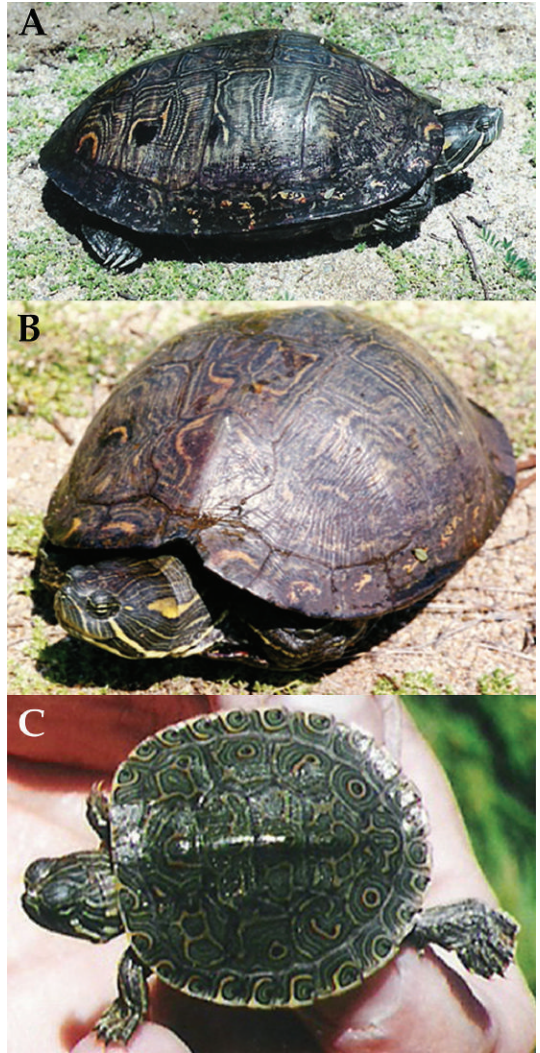


FIGURE 3. *Trachemys* from near Acapulco, Guerrero (All photos by JRB). A, B. Adult *T. venusta* from near Acapulco, Guerrero; C. Hatchling *T. venusta* from near Acapulco, Guerrero.

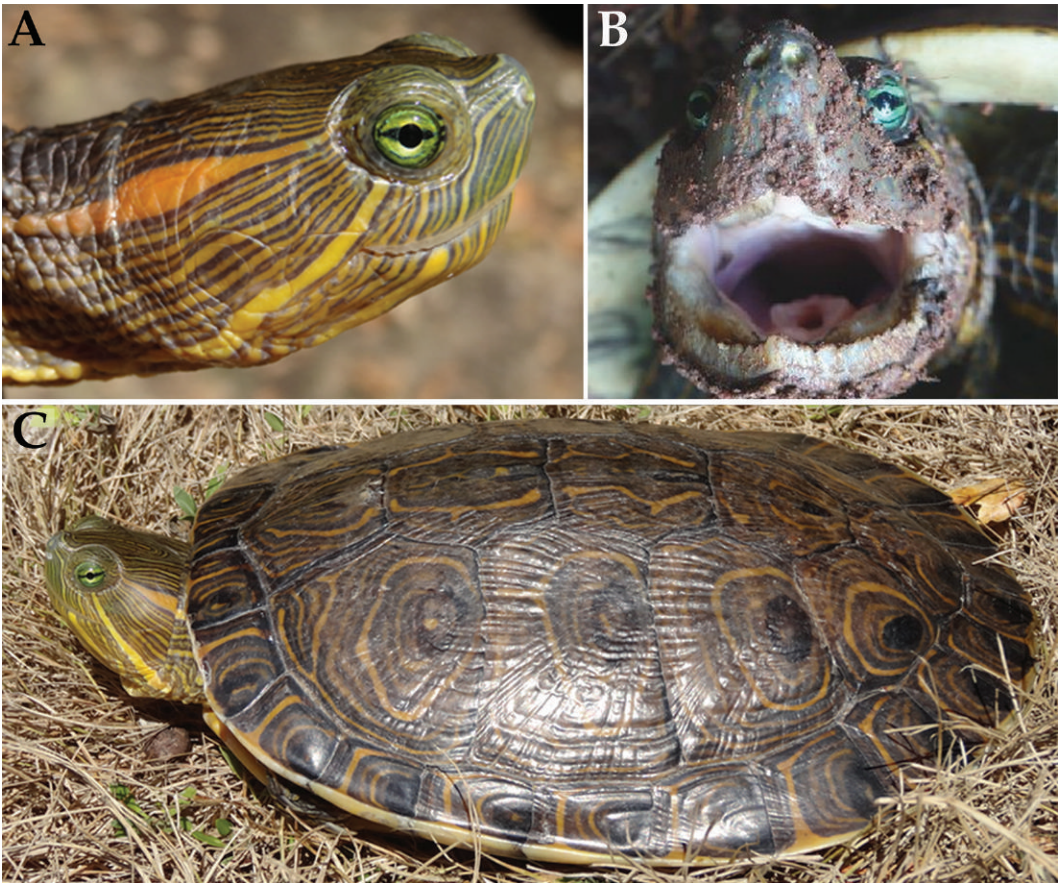


FIGURE 4. *Trachemys* from Northwestern Mexico showing the characteristic green/blue iris. A. *Trachemys ornata* from Sinaloa (Photo by JFP); B. *Trachemys ornata* from Punta Raza, Nayarit (Photo by Paulino Ponce-Campos); C. *Trachemys* from Sinaloa also showing dorsal shell coloration (Photo by JFP).

locality: Honduras) is considered the appropriate name for populations in the Atlantic drainages of Mexico and Central America (and Pacific drainages of the Isthmus of Panama). Ultimately, there is much work to be done to develop a stable nomenclature for Mexican and Central American *Trachemys*. Genomic data sets and denser geographical sampling including vouchers (McCranie et al. 2013; Rocha et al. 2014) are needed. Until these data are collected and analyzed, the species or subspecies level of some taxa will remain open to interpretation.

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## Appendix

Sequences generated for this study (for samples 10–14, 21–29) can be found under the GenBank Accession numbers (KR231017–KR231044). Museum vouchers for genetic sequences used in this study. Museum abbreviations: CAS, California Academy of Sciences Herpetology Collection, San Francisco, California, USA; CZACC, Colecciones Zoológicas del Instituto de Ecología y Sistemática, Havana, Cuba; IBH, Instituto de Biología Herpetology Collection, Universidad Nacional Autónoma de México, Mexico City, Mexico; MNHN, Museo Nacional de Historia Natural, Santo Domingo, Dominican Republic; MTD, Museum of Zoology, Senckenberg Dresden, Germany; MHUL, Museo Herpetológico de la Universidad Nacional Autónoma de Nicaragua, León, Nicaragua; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, USA; SMF, Naturmuseum Senckenberg, Frankfurt, Germany; TCWC, Texas Cooperative Wildlife Collection, Texas A&M University, College Station, Texas, USA; FLMNH, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA. Vouchers are whole-body preserved specimens except for samples from Fritz et al. (2012:15, 16, 31, and 32). Outgroup: *Pseudemys gorzugi* (MVZ 265706); 1. *T. gaigeae* (MVZ 265710); 2. *T. s. elegans* (TCWC 68553); 3. *T. s. elegans* (MVZ 265717); 4. *T. d. decussata* (CZACC 4.12777); 5. *T. d. angusta* (MVZ 265781); 6. *T. terrapen* (CAS 244098); 7. *T. decorata* (MNHN 23.873-10); 8. *T. s. vicina* (CAS 238933); 9. *T. s. stejnegeri* (CAS 249623); 10. *T. n. nebulosa* (MVZ 137443); 11. *T. n. hiltoni* (CAS 257535); 12. *T. n. hiltoni* (IBH 29755); 13. *T. n. hiltoni* (CAS 257534); 14. *T. n. hiltoni* (IBH 29759); 15. *T. dorbigni* (MTD T 5124, tissue only; Fritz et al. 2012); 16. *T. adiutrix* (MTD T 5115 [tissue only], Fritz et al. 2012); 17. *T. grayi* (MVZ 263975); 18. *T. emolli* x *venusta* (MVZ 233245); 19. *T. emolli* (MVZ 263793); 20. *T. emolli* (MVZ 263795); 21. *T. ornata* (CAS 257528); 22. *T. ornata* (IBH 29757); 23. *T. yaquia* (CAS 257531); 24. *T. yaquia* (IBH 29758); 25. *T. taylori* (MVZ 269714); 26. *T. taylori* (IBH 29756); 27. *T. hartwegi* (CAS 257525); 28. *T. hartwegi* (MVZ 269711); 29. *T. hartwegi* (IBH 29755); 30. *T. venusta venusta* (MVZ 264176); 31. *T. "ornata"/venusta* (MTD T 6041 [tissue only], Fritz et al. 2012); 32. *T. "ornata"/venusta* (MTD T 6042 [tissue only], Fritz et al. 2012); 33. *T. venusta cataspila* (IBH 25690); 34. *T. venusta venusta* (SMF 88199); 35. *T. venusta venusta* (MVZ 263395); 36. *T. venusta venusta* (UF 150886); 37. *T. venusta venusta* (MHUL 010); 38. *T. venusta venusta* (MHUL 009).

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**A New Grenadier Fish of the Genus *Lucigadus*  
(Macrouridae, Gadiformes, Teleostei) from the  
Emperor Seamounts, Northwestern Pacific**

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*Lucigadus borealis* sp. nov. is described from seven specimens collected in 409 m on Koko Guyot of the Emperor Seamounts chain. It represents the seventh and the most-northerly species of the genus. The new species is most similar in overall characters to *L. nigromarginatus* Smith and Radcliffe, 1912 of the Philippines, but is readily distinguished by the higher counts of pelvic-fin rays and gill rakers. So far as we know, 15 species of grenadiers (in two families and nine genera) are found on the Emperor Seamounts, but the taxonomic status of three of those are yet to be determined. Four of the 15 species are endemic to the seamount chain, two are also found on the Kyushu-Palau Ridge, and one is also found in Hawaii.

The floor of the North Pacific Ocean is marked by a prominent divide of volcanic islands and undersea elevations — the Hawaiian-Emperor Ridge (H-E) — that stretches almost 5,800 km from its origin in the Hawaiian Islands towards the northwest and north to its terminus near the juncture of the Kuril-Kamchatka and Aleutian trenches (Fig. 1). This ridge developed as a succession of volcanoes that formed as the Pacific Plate moved in a northwesterly direction over a hotspot in the earth's mantle under the active volcano Loihi, located about 30 km off the southeast coast of the island of Hawaii (Clague and Dalrymple 1989:8). The volcanoes subside as they move westerly on the Pacific Plate and reach sea level at approximately 24°N, where they become atolls. Coral growth keeps the atolls at sea level until they reach approximately 29°N; farther north, continual subsidence and bioerosion reduce coral growth leading to drowning or extinction of the atolls and eventual formation of drowned guyots (Grigg 1997). The Hawaiian Ridge is that part of the H-E that runs in a generally northwesterly direction about 3,450 km from the Hawaiian Islands to approximately 173°E, where the ridge takes a sharp turn to the north. The northerly portion of the H-E (about 2,300 km long), roughly paralleling longitude 170°E and consisting entirely of submerged volcanoes and guyots, constitutes the Emperor Seamounts. It is the oldest and most eroded part of the H-E, with the volcanoes at the northwestern end about 75 to 80 million years old (Clague and Dalrymple 1989:5).

Koko Guyot, a large guyot originally charted and named by Davies et al. (1972), is situated at 35°30'N, 171°45'E, near the southern end of the Emperor Seamounts. Its base lies at roughly 2,000–2,200 fathoms (ca. 3,600–4,960 m); its flat summit is less than 360 m deep and measures about 50 x 13 nautical miles (Davies et al. 1972:313). A reef limestone cap on the guyot provides evidence of the summit having once been close to sea level, since “reef-building corals and algae only flourish in depths less than about 30 fathoms [55 m], although they can survive down to about 85 fathoms [155 m]” (Davies et al. 1972:315).

Commercial trawling over the Emperor Seamounts was begun by vessels of the USSR in 1967

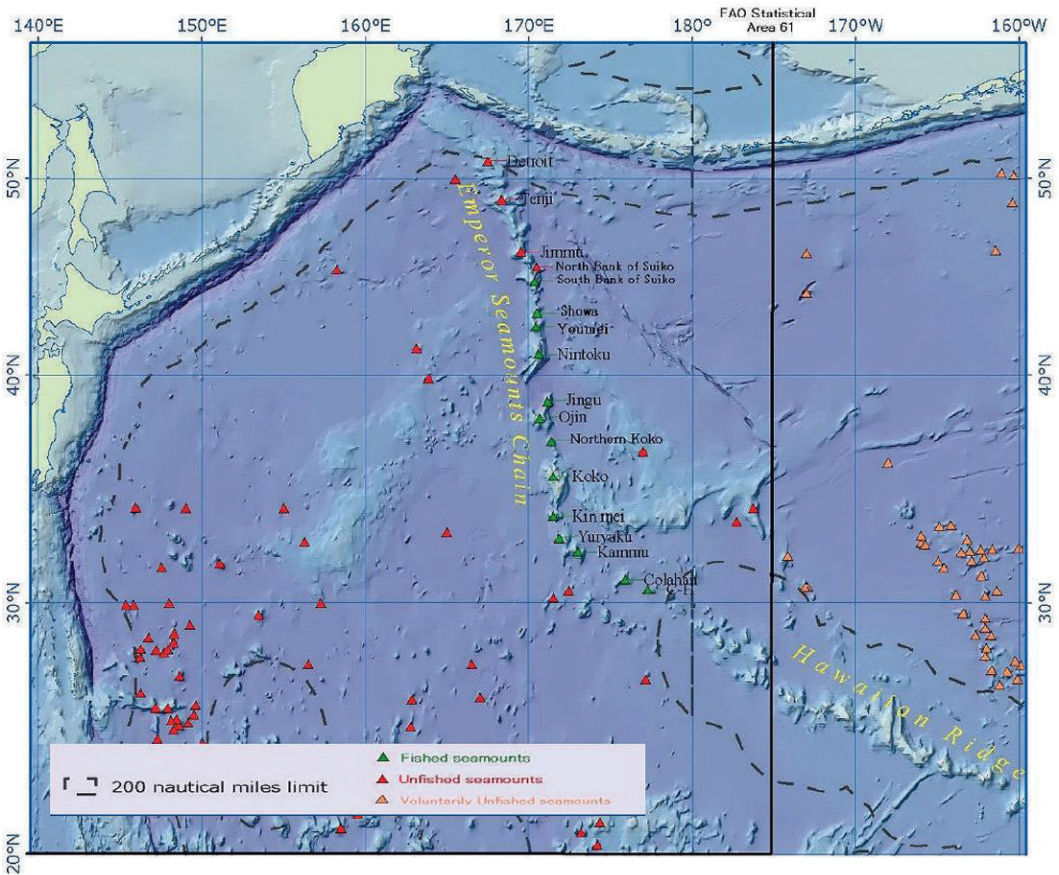


FIGURE 1. Emperor Seamounts chain in the northwestern Pacific, extending north-south along approximately the 170° meridian from about latitude 55°N southward to 30°N. (<http://nwpbfo.nomaki.jp/fisheries.html>)

and was followed in 1969 by Japanese trawlers conducting exploratory fishing surveys over several seamounts. The exploratory surveys led to the development of a limited commercial fishery targeting North Pacific Armorhead, *Pseudopentaceros wheeleri* Hardy, 1983, but catches of the species by Russian and Japanese vessels declined precipitously by the mid-1970s, and the fishery shifted to the Splendid Alfonsin, *Beryx splendens* Lowe, 1834. Low stock levels of *P. wheeleri* continued until 1992 when a strong year class was recruited. However, after only two years, the heavy fishing pressure drastically reduced the stocks. A similar phenomenon followed a good recruitment year in 2004. (Mostly extracted from Fisheries Agency of Japan, 2008.)

Concern by the international community over the possible negative impacts of bottom-fishing and precious-coral harvesting on vulnerable marine ecosystems (VME) in the high seas led to multilateral discussions in 2006 on the impacts of bottom fishing on the H-E seamounts, with participation by Japan, the Republic of Korea, the Russian Federation, and the United States. Interim measures were adopted for the Northwest Pacific in 2007 to address these concerns. In 2009, Canada, China, Faroe Islands, and Taiwan joined the negotiations. One of the agreements made during these and subsequent meetings was for scientific observers to be aboard trawler vessels to collect data and samples. (Extracted from North Pacific Fisheries Commission, 2015.)

Among a collection made by a scientific observer during a trawl survey on the Koko Guyot in



June 2011 were seven specimens of a species of *Lucigadus* Gilbert and Hubbs, 1920, family Macrouridae. Comparisons of these specimens with the six known species in the genus showed differences from all of them, suggesting that these Emperor Seamount specimens represented an undescribed species of the genus. The specimens are notable in having come from farther north than any known species of the genus. It is the purpose of this paper to describe the new species, record the most northern capture of the genus, and to record the rather unique nature of the grenadier fauna of the Emperor Seamounts.

## MATERIALS AND METHODS

Specimens used in this paper (notably for the comparative data in Table 1) are deposited in numerous institutional collections, some of which were visited by the first author many years ago. These include, but are not limited to, the Australian Museum (AMS), Academia Sinica Institute of Zoology of Taiwan (ASIZP), British Museum (Natural History) (BMNH), California Academy of Sciences (CAS), Institute für SeeFischerei, Hamburg (ISH), Natural History Museum of Los Angeles County (LACM), Muséum national d'Histoire naturelle, Paris (MNHN), Museum of New Zealand Te Papa Tongawera (NMNZ), Museum of Victoria (NMV), National Science Museum of Japan (NSMT), U.S. National Museum of Natural History (USNM), Zoologisch Museum, University of Amsterdam (ZMA). The reader is referred to Eschmeyer's *Catalog of Fishes* online version (updated 5 Feb. 2014) where Fricke and Eschmeyer's *A Guide to Fish Collections in the Catalog of Fishes* is available for institutional abbreviations and the current status of certain collections (e.g., the ISH collection is now in the Zoologisches Institute und Museum, Universität Hamburg (ZMH) with new catalog numbers; ZMA collection is now in Naturals Biodiversity Center, Leiden). Scientific names with author and date of the grenadiers mentioned in the text are provided in list of grenadiers from the Emperor Seamounts and the key to species of *Lucigadus*; complete references and taxonomic status for these species are provided in Eschmeyer's *Catalog of Fishes*.

Methods for making counts and measurements follow Gilbert and Hubbs (1916:147–148), with some procedures slightly modified as described in Iwamoto and Sazonov (1988:36–38). Abbreviations for fins are 1D and 2D – first and second dorsal fins, P – pectoral fin, V – pelvic fin, A – anal fin; GR-I and GR-II refer to gill rakers on the first and second arches, GR-I (outer) and GR-I (inner) refer to the lateral and mesial (or inner) series of rakers on the first gill arch.

## TAXONOMY

### Genus *Lucigadus* Gilbert and Hubbs, 1920

*Lucigadus* Gilbert and Hubbs, 1920:553 (as subgenus of *Ventrifossa*; type species *Macrourus lucifer* Smith and Radcliffe, 1912, by original designation).

*Lucigadella* Gilbert and Hubbs, 1920:552 (as subgenus of *Ventrifossa*; type species *Macrourus nigromarginatus* Smith and Radcliffe, 1912, by original designation).

*Ventrifossa* subgenus *Lucigadus*: Iwamoto, 1979:152–153 (characterization of three subgenera of *Ventrifossa*).

*Lucigadus*: Sazonov, 1985:17 (*Lucigadus* elevated to genus; discussion of relationships).— Iwamoto and Anderson, 1994:16.— Iwamoto and Merrett, 1997:526.

**DIAGNOSIS.**— Spinous second ray of first dorsal fin finely serrated along leading edge. Snout smoothly rounded, not pointed and prominently projecting beyond mouth. Anus closer to pelvic-fin insertion than to anal-fin origin; anus surrounded by a broad naked margin and preceded by two small naked fossae, the anteriormost fossa between pelvic-fin bases. Ventral region of body appearing to have shifted anteriorly so that gill membranes unite below eyes; pelvic-fin origin below oper-

cle. Suborbital region covered with several rows of small, unmodified scales; no sharp longitudinal ridge developed. Underside of snout fully scaled; no stout tubercular scale at tip and lateral angles of snout; small scales present on lowermost branchiostegal rays. Body scales with short, conical spinules, usually arranged in parallel rows. Dentition in upper and lower jaws small, in bands; premaxillary tooth band not extending beyond maxillary process of bone.

**REMARKS.**— With the new species herein described, the genus *Lucigadus* now includes seven species. (*Macruroplus potomus* Pequeño, 1971 is tentatively considered a synonym of *L. nigromaculatus* based on our examination of five specimens from Chile.)

#### Key to the species of *Lucigadus*

- 1a. Pelvic-fin rays 7–12, rarely 13, if 12 or 13 the body with broad darkish bands that extend onto margins of anal fin . . . . . 2
- 1b. Pelvic-fin rays usually 12–18, if 12 or 13, body lacking broad darkish bands and anal fin lacking alternate stretches of dark and light margins . . . . . 5
- 2a. Pelvic-fin rays 7 or 8; inner gill rakers on first arch 7–9; interorbital width 36–40% HL . . . . . *Lucigadus lucifer* Smith and Radcliffe, 1912
- 2b. Pelvic-fin rays 9–12; inner gill rakers on first arch 9–12; interorbital width 22–35% HL . . . 3
- 3a. Pelvic-fin rays 11–12, rarely 13; body crossed by broad bands, with bands extending onto dorsal- and anal-fin rays . . . . . *Lucigadus microlepis* Alcock, 1894
- 3b. Pelvic-fin rays 9–11; body lacking bands, anal and second dorsal fins relatively uniformly pigmented along their lengths . . . . . 4
- 4a. Snout length 24–28% HL; height of first dorsal fin 92–107% HL; distal tip of first dorsal fin blackish; anterior rays of anal fin with blackish distal margin . . . . . *Lucigadus nigromarginatus* Smith and Radcliffe, 1912
- 4b. Snout length 28–32% HL; height of first dorsal fin 108–129% HL; inter-radial membranes of anterior third of first dorsal fin blackish; anal fin lacking blackish distal margin . . . . . *Lucigadus acrolophus* Iwamoto and Merrett, 1997
- 5a. Length upper jaw 29–33% HL; length barbel 13–18% HL (rarely longer); length outer gill slit 13–17% HL; number of lateral-line scales from origin over distance equal to predorsal length 35–42; pyloric caeca 11–17 . . . . . *Lucigadus borealis* sp. nov.
- 5b. Length upper jaw 33–45% HL; length barbel 18–26% HL; length outer gill slit 18–31% HL; number of lateral-line scales from origin over distance equal to predorsal length 42–53; pyloric caeca 30–60 . . . . . 6
- 6a. Pelvic-fin rays 15–18 (rarely 13); length outer gill slit 18–21% (rarely 24%) HL; length upper jaw 33–39% HL; maximum size about 22 cm TL . . . . . *Lucigadus ori* Smith, 1939
- 6b. Pelvic-fin rays 13–15 (rarely 12); length outer gill slit 23–31% HL; length upper jaw 39–45% HL; maximum size attained more than 26 cm TL . . . . . *Lucigadus nigromaculatus* McCulloch, 1907

#### *Lucigadus borealis* Iwamoto and Okamoto, new species

Figures. 2a-b, Table 1

No literature refers to this species.

**DIAGNOSIS.**— A species of *Lucigadus* with 1D II,9–10; V 13–17; inner gill rakers on first arch 12–15; lateral-line scales over distance equal to predorsal length 35–42; pyloric caeca 11–17; length upper jaw 29–33% HL; length outer gill slit 13–17% HL. Body lacking dark bands or notable markings; anterior one-third or more of first dorsal fin blackish, with dark pigmentation sometimes more extensive distally; paired fins overall dark; anal fin almost entirely dark except

near base of anterior rays, especially in smaller individuals; rays of second dorsal and anal fins black near posterior tip of tail.

**TYPE-SPECIMENS.**— Holotype: CAS 237107 (female, 165 mm TL, 24.8 mm HL); Emperor Seamounts, Koko Guyot; 35°39'N, 171°01'E; 409 m; 14 June 2011. Paratypes (all collected with holotype): CAS 237109 (5: 18.5–29.0 mm HL, 113–198 mm TL); NSMT 237108 (1: 25.0 mm SL, 162 mm TL).

**DESCRIPTION.**— Counts and measurements of the type-specimens are provided in Table 1. General features of the fish are best seen in Figs. 2a-b. Head relatively short, approximately 15% of TL, somewhat longer than greatest body depth (under origin of first dorsal fin); tail greatly compressed, long and straplike, ending in a slender, almost-filamentous tip. Orbit slightly oval with long axis diagonal, greatest diameter more than length of snout and about equal to or slightly more than postorbital length; upper rim of orbit not entering dorsal profile. Snout broadly rounded in lateral view, with steep ventral profile; scarcely protruding beyond upper jaw and without acute ridges or sharp angles; no stout tubercular scales at tip and lateral angle. Suborbital region relatively flat and vertical, lacking a sharp, stoutly scaled longitudinal ridge. Mouth small, upper jaw about one-third or less of HL, extending posterior to point below anterior edge of pupil; lips relatively thick and fleshy, but not extremely so. Gill membranes narrowly connected across isthmus at point below middle of orbit. Chin barbel small, slender, its length about equal to narrowest width of sub-orbital (except in one small specimen of 18.1 mm HL where it was 27% of HL; others between 13% and 18% HL).

Origin of pelvic fin under opercle, pectoral fin slightly posterior to that vertical, and first-dorsal fin well behind that. Origin of anal fin under middle third of first dorsal fin. Height of first-dorsal fin about equal to HL, base of fin relatively steep and short (length of base about one-third or less of HL); pectoral and pelvic fins less than three-quarters of HL, none of the rays notably prolonged.



FIGURE 2a (above). *Lucigadus borealis* Iwamoto and Okamoto, sp. nov.. Holotype CAS 237107, lateral view. Koko Guyot, Emperor Seamounts.

FIGURE 2b (below). *Lucigadus borealis* Iwamoto and Okamoto, sp. nov.. Holotype CAS 237107, dorsal view. Koko Guyot, Emperor Seamounts. Scale bar = 1 cm.

Squamation typical of other members of genus, with small scales uniformly covering most of head. Gular membrane naked, but bases of ventral-most 1–3 branchiostegal rays have a few small scales. Body scales small, typically covered with 5–8 mostly parallel rows of short, erect, conical spinules with slightly recurved tips.

Teeth in both jaws small and in short wide bands, widest anteriorly; outer series of premaxillary teeth slightly enlarged.

Gill rakers short, tubercular, covered distally with minute spines. Gill arches connected by membrane at dorsal and ventral ends; the outermost and innermost gill slits greatly restricted.

Color in preservative overall light brown over dorsal aspects of head and trunk; bluish over abdomen and chest regions, with silvery reflections on ventral surfaces of trunk and head, and lateral face of pectoral-fin base. Dorsally, trunk darker than all of tail. Periproct and bases of pectoral and pelvic fins black; fin coloration otherwise as described in Diagnosis. Underside of head relatively pale, lips, chin barbel, and mouth lining pale; most inner surfaces of gill cavity immaculate, but outer margins and rims of first and fifth gill slits heavily punctate; gill filaments pale, but arches and gill rakers gray. Branchiostegal membranes rather heavily speckled, as are lateral and ventral surfaces of lower jaw, and to a lesser extent, the operculum. Heavy punctations on body seen in some other members of genus lacking in the new species.

**ETYMOLOGY.**— From the Latin *borealis*, northern, in reference to the northern distribution of the new species.

**COMPARISONS.**— *Lucigadus borealis* is most similar in overall appearance to *L. nigromarginatus* from the Philippines, Taiwan, and the East Indies, but the two species are readily differentiated by the latter having fewer pelvic-fin rays (10–11 vs. 13–17), fewer inner gill rakers on first arch (10–12 vs. 12–15), smaller orbit (30–36% HL vs. 36–45% HL), and longer upper jaw (33–39% HL vs. 29–33% HL). *Lucigadus lucifer*, *L. acrolophus*, and *L. microlepis* also have fewer pelvic-fin rays as well as other differentiating features (see Table 1); *L. microlepis* is unique in the genus in having a banding pattern on the body and on vertical fins. *Lucigadus nigromaculatus* and *L. ori* have high pelvic-fin ray counts like *L. borealis*, but neither of those two have such a short outer gill slit as *L. borealis* (13–17% HL vs. 18–31% HL), a short upper jaw (29–33% HL vs. 33–45% HL), and so few pyloric caeca (11–17 vs. 30–60). Unlike *L. borealis* with a dark anterior one-third or so of the first dorsal fin, *L. nigromaculatus* and *L. ori* have a prominent black blotch distally on the fin. (Note that we have treated *L. potronus* as a synonym of *L. nigromaculatus*.)

**DISTRIBUTION.**— The new species is known only from one collection in a bottom trawl in 409 m on the Koko Guyot located near the southern end of the Emperor Seamounts. The capture of *Lucigadus borealis* is from a latitude farther north than any previously recorded specimen of the genus *Lucigadus*. So far as we can ascertain, the most northern previous record of the genus is off Taiwan near the Tropic of Cancer at around 23°N (Chiou et al. 2004:45, for a *L. nigromarginatus* specimen misidentified by those authors as *Lucigadus lucifer*). There are no records of the genus from off Japan. Most other records of the genus are from tropical waters of the western Pacific or subtropical waters of the southern hemisphere including Australia, South Africa, and South America. With the exception of *L. borealis*, the genus is not known from the Pacific Plate.

**DISCUSSION.**— The fish fauna of the Emperor Seamounts is composed of many wide-ranging bathypelagic and thalassobathyal species of boreal waters in addition to a number of endemic species (Novikov et al. 1981; Borets 1986). Based on his study of fishes collected by Soviet vessels on eight seamounts of the Emperor Seamounts (“Northwestern range”) and eight of the Leeward Isles (“Hawaiian range”), Borets (1986) recognized six “biotypes” based on water mass and bottom relief, with each biotype having its own “ichthyocene,” viz., its characteristic species composition. Up to that time (1986), Borets found 80 fish species recorded from the Emperor

TABLE 1. Counts and measurements (in % HL except for total length and head length) of seven species of genus *Lucigadus* (*L. potronus* is considered a synonym of *L. nigromaculatus*, but data for four specimens are here provided separately). Absence of data for some counts and measurements resulted from those values not taken by first author in previous years, or damage to specimens precluded accurate measurements and counts. Abbreviations are explained in the Materials and Methods section of the text. Numbers within parentheses are those outside the range of most other specimens of the species.

	<i>lucifer</i>	<i>acrolophus</i>	<i>nigromarginatus</i>	<i>microlepis</i>	<i>nigromaculatus</i>	" <i>potronus</i> "	<i>ori</i>	<i>borealis</i>
Total Length	210-217	66-180	105-200	92+-155	192-339	140-262	120-202	113-198
Head Length	27-33	10.4-28.9	24-33	13.3-25.4	16.8-50	19.7-35.2	20.5-33	18.1-24.8
Snout Length	26-28	28-32	24-28	24-31	25-30	25-30	24-30	25-30
Preoral Length	19-21	18-25	17-22	18-24	18-22	18-19	(17)19-24	20-24
Internasal Width		23-28		19-27	18-23	20-21	(16)18-23	17-23
Interorbital Width	36-40	28-35	22-31	25-33	20-24	20-21	(19)23-26	23-28
Orbit Diameter	33-37	32-38	30-36	32-42	40-47	39-43	39-45	36-45
Suborbital Width	13-14	14-18	12~15	12~16	13-17	13-21	13-17	14-17
Postorbital Length	44-46	41-46	39-46	37-43	34-39	36-39	32-37	35-38
Orbit to Preopercle	40-41	36-44	34-39	34-38	30-33	31-35	28-32	30-34
Upper Jaw	37-39	35-41	33-39	34-40	39-42	39-45	33-39	29-33
Length Barbel	13-14	22-23	20-26	18-30	18-26	20-26	18-24	13-18(27)
Length 1st Gill Slit	19-23	19-23	17-21	18-23	23-31	25-27	18-21(24)	13-17
Preanal Length	140--	145-171	138-152	139-178	140-171	146-158	142-167	143-162
Isthmus to Anal Fin	73-76				65-87	89-107	81-98	80-94
Outer V to A Origin	41	42-59	41-53	34-58	38-52	36-54	(35)42-58	45-62
Body Depth (greatest)	102	91-114	79-115	89-113	97-112(124)	91-106	88-108	78-91
1D-2D Interspace	52	46-75	60-88	45-72	42-51 (59)	32-54	31-50	31-50
Height 1D	72-96	108-129	92-107	102-128	101-134	106-128	105-122	96-107
Length P	67	60-69	55-67	54-71	61-72	66-73	63-72	61-75
Length V		60-73	47-61	55-86	44-69	51-58	(45)49-62	44-58
<b>COUNTS</b>								
1D	11~12	9~11	9~12	10~11	10~11	10~11[9]	9~11	9~10
P	18-20	18-24	18-23	20-25	20-23	19-22	18-22(23)	19-20(21)
V	7~8	9~11	10~11	11~12(13)	13-15	13-14[12]	(13)15-18	13-16(17)
GR-I (outer)		7~9		8~10	9~11		8~10	8~11
GR-I (inner)	7~9	9~12	10~12	11~12	12~16	12~14	12~14	12~15
GR-II (outer)	8~8	8~11	9~11	10~12	12~15	12~14	12~13	11~14
GR-II (inner)		8~11		11~12			12~14	11~13
Scales 1D	14-17		13-16		17-20	16	13-16	11~14
Scales 2D	10~11	8.5-10	7~9.5	8.5-10	10~14	10~11	8~13	10~11
Scales Lateral Line	50-56	31-40	37-42	37-40	43-50	42-44	42-53	35-42
Pyloric Caeca					30(n~1)	32-57	60(n~1)	11~17
No. of specimens	3		8	5	11	4	17	7

Seamounts and 55 species from the Leeward Isles, with 39 species common to both regions; he listed only six grenadier species.

Wilson and Kaufmann (1987) provided a comprehensive review of the world's seamount biota and their biogeography. Of the 449 seamount fish species in 92 families that these authors found recorded in the literature and in unpublished sources, the grenadiers were best represented with 39 species. Subsequent to their work, many more fish species, including grenadiers, have been recorded from an expanded list of seamounts whose fauna has been sampled (see for example, Sazonov and Iwamoto 1992; Iwamoto and Merrett 1997; Merrett and Iwamoto 2000). Nevertheless, their basic assumptions of seamount biogeography remain valid. The most diverse families represented had many, and some exclusively, deepwater members, and "their importance probably reflects the fact that over 60% of the seamounts were sampled at greater than 300 m depth" (Wilson and Kaufmann 1987:364). These authors distinguished four main biogeographic categories in the seamount biota: (1) provincial — confined to the general region of the seamount; (2) widespread to cosmopolitan; (3) exotic — rarely or never before found in the immediate region; and (4) endemic — confined to a particular seamount or several seamounts of a particular group. One or another of the Emperor Seamounts grenadiers appears to fall into each of these categories.

Grenadiers of the Emperor Seamounts are represented by at least 15 species, including the new *Lucigadus* here described and the *Coelorinchus* species recorded by Sazonov (1994:111) from one specimen that he thought may be a variant of his new species *C. anisacanthus*. Subsequent to Sazonov's original description, the first author (TI) has examined five specimens of that "variant" at HUMZ; those specimens confirmed the morphological differences from *C. anisacanthus* that Sazonov found in his single specimen and are without much doubt an undescribed species. Two other species, a *Kuronezumia* and a *Nezumia*, both unidentifiable, were examined by TI in the collections of HUMZ in 2010.

Of the 15 grenadier species, four appear to be endemic: *Coelorinchus anisacanthus*, *Coelorinchus* sp. cf. *anisacanthus*, *Lucigadus borealis*, and *Nezumia tinro*. The unidentified *Kuronezumia* and *Nezumia* may also represent endemic species. *Lucigadus borealis* could also be categorized as an exotic species, in that it displays a highly disjunct distribution from its congeners, none of which are found in the immediate region.

Five species can be considered as provincial: *Nezumia obliquata*, known from off Kauai in the Hawaiian Islands and Ojin Guyot in the Emperor Seamounts; *Coelorinchus matsubarai* known from the Kyushu-Palau Ridge and the Emperor Seamounts (Kammu Guyot and Koko Guyot; and also Colahan Seamount in the Northwestern Hawaiian Islands, although that seamount is sometimes considered part of the Emperor Seamounts [see Wikipedia 2014]); *Hymenocephalus hachijoensis* from the Kyushu-Palau Ridge and the Emperor Seamounts (Kammu Guyot and Nintoku Guyot); and *Coelorinchus gilberti*, a species with a peculiar distribution for a *Coelorinchus* of the North Pacific Ocean, ranging from southern Japan (33°N) north to off Hokkaido and also off the Kyushu-Palau Ridge and the Emperor Seamounts (32°41.6'N, 172°18.8'E, Yuryaku Guyot; 5 specimens, HUMZ 132360 to 132364). *Bathygadus antrodes* is somewhat exceptional in ranging from off Okinawa to central Japan (Honshu) to the Emperor Seamounts (Nintoku Guyot).

The remaining species are in the widespread category (but not cosmopolitan) and appear to have broad distributions in boreal waters of the North Pacific. Wilson and Kaufmann (1987:369) describe a faunal component of the Emperor Seamounts whose species follow the Pacific rim from northern Japan to northern Baja California. They provide as examples two grenadiers, *Albatrossia pectoralis* and *Coryphaenoides acrolepis*, to which should be added *C. cinereus* and *C. filifer*. The first two species have a disjunct distribution having also been recorded from the southwestern Atlantic off the Falkland Islands (Brickle and Laptikovskiy 2002; Laptikovskiy et al. 2013). *Alba-*

*trossia pectoralis* has also been captured in the western Pacific well to the south of Japan at Iwo Retto or Volcano Is. (24°12'N, 149°58'E, about 750 n.mi. ne. of the Mariana Trench National Marine Sanctuary in 1200 m; HUMZ 71918). That species has a long pelagic larval stage (see Endo et al. 2010), and juveniles do not become benthopelagic until attaining about 51–55 cm TL (Orlov and Tokranov 2008). *Coryphaenoides longifilis* more or less follows a Pacific-rim distributional pattern except that it has not been recorded in the eastern North Pacific, aside from the Bering Sea.

What seems evident with the widespread species (and the exceptional *Bathygadus antrodes* and *Coelorinchus gilberti*) is that they have followed the pathway provided by the Emperor Seamounts to extend their distributions along the continental margins southward and deep into the North Pacific basin. These species may use seamounts along a chain as stepping stones, a hypothesis suggested by Hubbs (1959) and further supported by Wilson and Kaufmann (1987) for seamount species exhibiting trans-oceanic dispersal. Some grenadiers appear to have long-lived pelagic larvae and juveniles, which with propitious currents could allow widespread dispersal to the limits of their physical and physiological tolerances. Arkhipkin et al. (2010) have postulated an antipodal link between the North Pacific and South Atlantic based on changes in deep-water circulation patterns. *Albatrossia pectoralis* and *Coryphaenoides acrolepis* are possible candidates in this category; Laptikovskiy et al. (2013) have suggested that such changes in deep-water circulation patterns create a “deepwater conveyor” that could transport the fish through the South Pacific, around Cape Horn, and into the South Atlantic.

### List of Species of Macrouridae and Bathygadidae recorded from the Emperor Seamounts

#### Family Bathygadidae

*Bathygadus antrodes* (Jordan and Gilbert, 1904). Sazonov (1994:100–101) recorded five specimens from the Nintoku Guyot (41°05'N, 170°43'E; 1120–1160 m); before then, it was known only from off central Japan and Okinawa.

#### Family Macrouridae

*Albatrossia pectoralis* (Gilbert, 1892). HUMZ 71918; east of Iwo Retto (Volcano Is.) (24°12'N, 149°58'E) in 1200 m; 1977.10.9. The genus name *Albatrossia* is used here, although the genus is treated by most recent authors as a junior synonym of *Coryphaenoides*.

*Coelorinchus anisacanthus* Sazonov, 1994. ZMMGU P18251 (holotype) and P18252 (13 paratypes, 270–300 mm TL); Koko Guyo (35°21'N, 171°19'E) in 550 m. Five additional specimens were examined by TI in HUMZ.

*Coelorinchus gilberti* Jordan and Hubbs, 1925. HUMZ 132360 to 132364 (87–159 mm HL, 315–400 mm TL); near Yuryaku Guyot (32°41.6'N, 172°18.8'E) in 644 m; 1993.11.7.

*Coelorinchus matsubarai* Okamura, 1982. HUMZ 68719 (63.2 mm HL, 250+ mm TL); (locality uncertain, probably Emperor Seamounts). HUMZ 132368 and 132369; Koko Guyot (35°53.8'N, 171°20.1'E) in 385–384 m; 1993.11.3. HUMZ 68815–68818 (4 paratypes, 228–240 mm TL); Kimmei Seamount (35°21.6'N, 171°41.4'E) in 330 m; 1977.7.28 (reported by Okamura 1982:167).

*Coelorinchus* sp. cf. *anisacanthus* [see Sazonov, 1994]. ZMMGU P18250 (93 mm HL, 338 mm TL); Koko Guyot (34°48'N, 171°47'E) in 820 m; 1984.08.25.

*Coryphaenoides acrolepis* (Bean, 1884). HUMZ 71889; Yomei Guyot (42°18'N, 170°23'E) in 890–1030 m; 1977.9.16. HUMZ 71995 and 71996; near Nintoku Guyot (40°58'N, 170°40'E) in 1080–1100 m; 1977.6.28. HUMZ 72013; Ojin Guyot (37°55'N, 170°22'E) in 1055–1100 m; 1977.9.11. 1984.7.25. HUMZ 85058 (78.5 mm HL); Yomei Guyot (42°23.0'N, 170°23.7'E) in 1240–1500 m; 1979.7.22.

*Coryphaenoides cinereus* (Gilbert, 1895). HUMZ 85058; Yomei Guyot (42°23'N, 170°23.7'E) in 1240–1500 m; 1979.7.22. HUMZ 85147; Nintoku Guyot (41°09.3'N, 170°37.8'E) in 1080–1100 m; 1977.6.28.

*Coryphaenoides longifilis* (Günther, 1877). HUMZ 71903, 71904 and 71905; Ojin Guyot (38°00'N, 170°18'E) in 920–1080 m; 1977.7.17.

- Hymenocephalus hachijoensis* Okamura, 1970. This species was originally described from two specimens taken on the northern part of the Bonin Ridge (33°16'05"N, 140°03'06"E). Sazonov (1994:102) recorded the species from two Emperor Seamounts specimens from near Milwaukee Seamount Group: Kammu Guyot (32°N, 173°E) and Nintoku Guyot (41°04'N, 170°32'E) in 1050–1060 m, and one from the Kyushu-Palau Ridge
- Kuronezumia* sp. HUMZ 132366 and 132367; near Koko Guyot (35°12.6'N, 170°37.8'E) in 1022 m; 1979.7.23.
- Lucigadus borealis* Iwamoto and Okamoto, new species
- Nezumia obliquata* Gilbert, 1905. This species was originally described from a single juvenile (155 mm long) taken off Kauai, Hawaii. Sazonov (1994:103–104, Fig. 2) recorded it from Ojin Guyot (37°55'N, 170°53'E) in 1400–1240 m.
- Nezumia tinro* Sazonov, 1985. ZIL 47136 (holotype, m53 mm HL, 294+ mm TL); Yomei Guyot (44°30'N, 171°31'E) in 1250–1260 m; 1976.10.10. ZIL 47137 (paratype, 46 mm HL, 273+ mm TL); Yomei Guyot (42°14.6'N, 170°22'E) in 1320 m; 1976.10.13. ZMMGU P18246 (13 spec., 128–360 m TL); Ojin Guyot (37°51'N, 170°53'E) in 1,400–1,240 m. HUMZ 71913 (41.0 mm HL, 200+ mm TL) and HUMZ 85083 (1 spec.); Emperor Seamounts [locality information not available].
- Nezumia* sp. HUMZ 70716, 70717, 70718, 70719: Emperor Seamounts. [locality information not available]. HUMZ 85149, 85150, 85151; Nintoku Guyot (41°09.3'N, 170°37.8'E) in 1022 m; 1979.7.23. HUMZ 85082, 85083, 85084; Jingu Guyot (38°42.3'N, 171°06.9'E) in 820 m; 1979.7.24.

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**A Taxonomic Review of the Northwestern Nearctic Subgenus *Pseudonomaretus* Roeschke 1907, including Description of the New Species *Scaphinotus hoodooensis* (Coleoptera: Carabidae: Cychrini) from the Bitterroot Mountains of Montana**

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**A new species in the cychrine genus *Scaphinotus*, subgenus *Pseudonomaretus*, *S. hoodooensis*, is described from the Bitterroot Mountains of western Montana (type locality: 0.5 miles N of Hoodoo Pass, Mineral County). A key is provided for identification of adults of all five species in the subgenus, and a lectotype is designated for *Cychnus idahoensis* Webb, a junior synonym of *Scaphinotus merkelii* (G. Horn). Phylogenetic relationships with other subgenera of *Scaphinotus* are briefly discussed.**

**KEYWORDS:** Coleoptera; Adephaga; Carabidae; Cychrini; *Scaphinotus*; *Pseudonomaretus*; new species; Bitterroot Mountains

It was late in the afternoon of August 16, 1988 when the first author [DHK] and his family stopped at the crest of the Bitterroot Mountains on the border between Idaho and Montana at Hoodoo Pass (Pl. 1). It had been a long day for the family, having endured many hours of waiting in the van or otherwise occupying themselves while DHK collected beetles at several sites along Forestry Road 250 on the Idaho side of the range. It was still a long drive down the Montana side to where they hoped to have dinner and spend the night somewhere along the Clark Fork River. Permission for one last collecting stop, at this place with an intriguing name and a beautiful view, was requested and granted, but only for “10 minutes”. As DHK stepped out of the van, he was attacked by a swarm of hungry mosquitoes. It would be a quick stop. A frenzied turning of stones and a rolling of logs ensued. Then, under a flat slab of wood within 20 meters of the car, he found something unexpected — a beautiful, metallic purple adult carabid beetle of the genus *Scaphinotus*, species unknown but most likely something new and undescribed. Collecting resumed with renewed vigor, but no additional specimens were found in the time remaining.

It would be another eight years, until August 1996, before DHK would return to Hoodoo Pass and, with more time available, collect a large enough series to be sure that the original specimen indeed represented a new and undescribed species. Since then, our detailed examination of features of the specimens at hand, use of available keys (Ball 1960; Ball and Bousquet 2001; Gidaspow 1973; Hatch 1953; Lindroth 1961) and comparisons with representatives of all the other described species of *Scaphinotus* has suggested that this new species is a member of subgenus *Pseudonomaretus* Roeschke (1907), but one with a unique combination of structural features. Gidaspow (1973) reviewed the subgenus and its taxonomic history and summarized morphological and distributional data for the four included species known to her. Bergdahl (2014) provided a good summary of current knowledge about those same four species. The purpose of our report is to describe

PLATE I



Photograph of habitat at type locality of *Scaphinotus hoodoensis*: Kavanaugh and Angel sp. nov., 0.5 miles N of Hoodoo Pass, Mineral County, Montana.

this new species and provide a new key to adults of *Pseudonomaretus* species. We also take this opportunity to provide a lectotype designation for *Cychnus idahoensis* Webb, a junior synonym of *Scaphinotus merkelii* (G. Horn), and briefly discuss possible phylogenetic relationships of the subgenus.

#### MATERIALS AND METHODS

**MATERIALS.**— A total of 332 specimens representing *Scaphinotus* (*Pseudonomaretus*) species were examined during this study, including the primary type specimens for *Cychnus merkelii* G. Horn and *Cychnus idahoensis* Webb. Hundreds of additional specimens representing other cychnine genera and species were also examined in the course of this study. Codens used in this report for collections from which specimens were borrowed and/or in which specimens, including primary types, are deposited are as follows:

CAS	California Academy of Sciences, San Francisco, U.S.A 94118
CNC	Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario, Canada K1A 0C6
JRL	James R. LaBonte, personal collection, Dallas, OR, U.S.A. 97338
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A. 02138
NMNH	Department of Entomology, United States National Museum of Natural History, Smithsonian Institution, Washington, D. C., U.S.A. 20013-7012
WSU	M. T. James Entomological Collection, Washington State University, Pullman, WA, U.S.A 99164-6382

**EXAMINATION OF SPECIMENS.**— Specimens were examined using a Leica MZ9.5 stereoscopic microscope with a Proline 80 LED Ring Illuminator.

**MEASUREMENTS.**— Measurements were made using a Leitz stereoscopic dissecting microscope with a calibrated ocular grid with a scale interval of 0.1 mm. The only measurement used in this report is: standardized body length (SBL), which equals the sum of the lengths of the head (measured from the apex of the clypeus to a point on the midline at the level of the posterior margin of the compound eyes), pronotum (measured from the apical margin to the basal margin along the midline), and elytra (measured along the midline from the apex of scutellum to the apex of the longer elytron).

**DISSECTIONS.**— Male and female genitalia were extracted from specimens relaxed in water immediately after it had boiled and to which a few drops of liquid detergent had been added. Genitalic preparations were then cleared in hot 10% potassium hydroxide solution for five to 10 minutes, each constantly monitored to achieve only a useful degree of clearing. They were then rinsed briefly in 10% acetic acid and then repeatedly in distilled water. After examination, preparations were stored in glycerin in polyethylene microvials and pinned beneath their specimens of origin.

**ILLUSTRATIONS.**— Digital images of whole specimens and particular structures were taken using a Leica imaging system including an M165C dissecting microscope, DFC550 video camera, and two KL1500 LCD light sources. Stacked images were captured and combined into single montage images using the Leica Application Suite V4.2.0. Plates of images were created using Adobe Photoshop CS5.

## SYSTEMATICS

***Scaphinotus* Dejean 1826***Scaphinotus* Dejean 1826:17. Type species: *Carabus elevatus* Fabricius 1787, by monotypy.**Subgenus *Pseudonomareus* Roeschke 1907***Pseudonomareus* Roeschke 1907:154. Type species: *Cychrus relictus* G. H. Horn 1881; designated by Casey 1914:30.

**RECOGNITION.**— Throughout the taxonomic history of this subgenus, it has proven difficult to provide a suite of diagnostic features that are shared by all of its members; and the combination of features shared by members of our new species confounds the problem even more. Keys provided by Ball (1960), Gidaspow (1973), and Ball and Bousquet (2001) all required *Pseudonomareus* to key out in two separate couplets. Hatch (1953) cited the combination of moderately widened genal projections, distinct elytral striae and broadly dilated male protarsi as characteristic of members of *Pseudonomareus*. However, he dealt only with *Scaphinotus* species of the Pacific Northwest and so did not have to distinguish *Pseudonomareus* members from those of *Maronetus* Casey (1914) or *Nomareus* LeConte (1853), at least some members of which share these same features. In his treatment of *Scaphinotus*, Lindroth (1961) avoided the problem entirely by keying specimens directly to species, without reference to subgenera.

Adults of all species in this subgenus share the following combination of character states: head with frons smooth, convex, not cristate; genae expanded laterally as a narrow shelf in front of and below each eye, each with a distinct notch in the shelf in line with the anterior margin of the eye; labrum deeply emarginate, with four setae at base between lateral lobes; labial palpomere 2 with three or more setae; pronotum with base impunctate; elytral epipleura impunctate or with only a few scattered, shallow, vaguely defined depressions; anterior tarsus of male with tarsomeres 1 to 3 broadly expanded laterally and with dense pads of disco-type (Stork 1980) adhesive setae ventrally. This combination of features is not sufficient to distinguish all members of *Pseudonomareus* from all members of all other subgenera. There are several additional features shared by members of most but not all species of *Pseudonomareus*, and these are presented and considered in the Discussion section below. Combined, the features shared by all members plus those shared by most members represent a character complex that is unique to this taxon among cychrine genera and subgenera. So characterized, *Pseudonomareus* is a classic example of a “polythetic taxon” as discussed by Mayr (1969).

**Key to Species of *Scaphinotus* Subgenus *Pseudonomareus* Roeschke**

- 1a SBL 12.5 mm or less; elytra moderately shiny, with or without faint bronze or distinct metallic purple reflection . . . . . 2
- 1b SBL 13.0 mm or more; elytra dull or slightly shiny, without metallic reflection . . . . . 3
- 2a Head with a distinct transverse impression at level of posterior margin of eye clearly delineating frontal and occipital regions, antennomere 4 (Fig. 3b) as pubescent as antennomere 5 or nearly so; labrum (Fig. 2b) with lateral lobes markedly long and narrow; male protarsomere 1 (Fig. 5b) with pad of adhesive setae ventrally on apical two-thirds only, protarsomere 4 also with a pad; elytra without or with only very faint bronze metallic reflection, without discal setiferous pores on intervals 4 and 8 . . . . . *Scaphinotus merkelii* (G. H. Horn)
- 2b Head without or with only a very faint transverse impression at level of posterior margin of eye, frontal and occipital regions more or less continuous dorsally; antennomere 4 (Fig. 3a) not

as pubescent as antennomere 5, with only a few scattered setae, mainly in apical half; labrum (Fig. 2a) with lateral lobes moderate in length and width; male protarsomere 1 (Fig. 4b) with pad of adhesive setae ventrally over virtually entire ventral surface, protarsomere 4 without a pad; elytra (and also pronotum in some individuals) with distinct purple or bronze (in a few specimens) metallic reflection . . . . *Scaphinotus hoodooensis* Kavanaugh and Angel, sp. nov.

- 3a Labrum (Fig. 2e) with lateral lobes markedly long and narrow; pronotum narrow, widest at or near middle, basolateral setiferous pores absent; median lobe of male genitalia as in Fig. 10 . . . . . *Scaphinotus mannii* Wickham
- 3b Labrum (Figs. 2c or 2d) with lateral lobes moderate in length and width; pronotum broad, widest distinctly anterior to middle, basolateral setiferous pores present; median lobe of male genitalia as in Figs. 11–12 . . . . . 4
- 4a Elytra with 13 regular striae, uninterrupted on elytral disc, less regular laterally in a few individuals; male with armature of internal sac of median lobe of aedeagus as in Fig. 11 . . . . . *Scaphinotus regularis* (LeConte)
- 4b Elytra with 13–16 apparent striae, with at least lateral striae disrupted by punctures in and between striae; male with armature of internal sac of median lobe of aedeagus as in Fig. 12. . . . . *Scaphinotus relictus* (LeConte)

***Scaphinotus (Pseudonomareus) hoodooensis* Kavanaugh and Angel, sp. nov.**

Figures 1, 2a, 3a, 4, 8, Pl. I

**TYPE MATERIAL.**— HOLOTYPE, a male, deposited in CAS, labeled: “U.S.A., Montana, Mineral County, Bitterroot Mts., 0.5 miles N of Hoodoo Pass, 1750 m.”/ “46°58.7’N/ 115°0.2.0’W, 4 August 1996, Stop # 96-43 D. H. Kavanaugh collector”/ “D. H. Kavanaugh collection” [orange label]/ “HOLOTYPE *Scaphinotus hoodooensis* Kavanaugh and Angel 2015” [red label]. A total 93 paratypes (62 males and 31 females): 35 males and 13 females (CAS, NMNH), same label data as holotype; 1 male (CAS) labeled “U.S.A., Montana, Mineral County, Bitterroot Range, Hoodoo Creek, 0.5 miles NW of Hoodoo Pass, 1780 m, 16 Aug. 1986, Stop #88-28 D. H. Kavanaugh collector”/ “D. H. Kavanaugh collection” [orange label]; 26 males and 18 females (JRL) labeled “MT Mineral Co.0.7 km NW of Hoodoo Pass. J.R. LaBonte 2 August 2014”/ “39.5 km SSW of Superior, 46.978750° N, -115.037000° W elev. 1,791 m” (JRL). All paratypes also bear the following label: “PARATYPE *Scaphinotus hoodooensis* Kavanaugh and Angel 2015” [yellow label]. Type locality. U.S.A., Montana, Mineral County, Bitterroot Mountains, 0.5 miles N of Hoodoo Pass.

**ETYMOLOGY.**— The specific epithet is a Latinized adjective in the masculine form based on the name of the type locality, Hoodoo Pass

**RECOGNITION.**— Adults of this new species are distinguished from those of other species of *Pseudonomareus* by the following combination of character states: size moderate, SBL = 12.5 mm or less; dorsal surface moderately shiny; elytra with distinct metallic purple reflection; head without or with only a very faint transverse impression at level of posterior margin of eye, frontal and occipital regions more or less continuous dorsally; antennomere 4 (Fig. 3a) not as pubescent as antennomere 5, with only a few scattered setae or very sparse pubescence in apical half; labrum (Fig. 2a) with lateral lobes moderate in length; male protarsomere 1 (Fig. 4b) with pad of adhesive setae ventrally over virtually entire ventral surface, protarsomere 4 without a pad; elytral intervals 4 and 8 with two or more discal setiferous punctures.

**DESCRIPTION.**— Dorsal habitus as in Fig. 1. Medium-sized for subgenus, SBL = 10.9-12.4 mm in males, 10.1–11.9 mm in females. Body color black to piceous, femora and tibiae black to



FIGURE 1. Dorsal habitus, male, *Scaphinotus hoodoensis* Kavanaugh and Angel sp. nov. Scale line = 1.0 mm. Ink and colored pencil drawing by Virginia ("Ginny") Kirsch.

piceous, tarsi piceous to rufopiceous; dorsal surface moderately shiny; microsculpture of head, pronotum and elytra isodiametric, shallowly impressed, with sculpticells on head a pronotum distinctly smaller than those on elytra; elytra with distinct metallic purple reflection (more faintly visible in a few specimens), pronotum also with faint metallic blue or purple reflection in some specimens.

*Head.* Frons smoothly convex, without punctures or wrinkles, without or with only a very faint



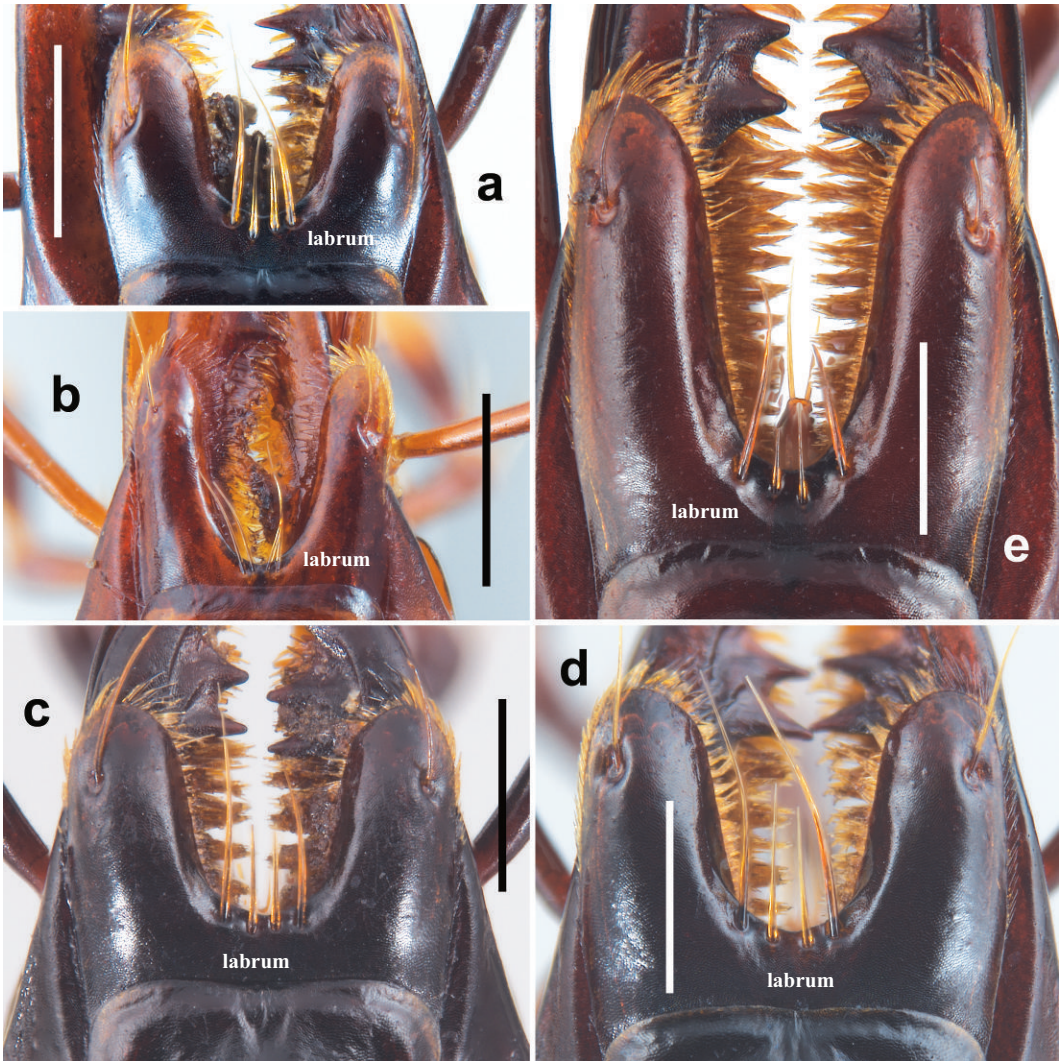


FIGURE 2. Digital photographs of labrum of *Scaphinotus* (*Pseudonomaretes*) species, dorsal aspect; a, *S. hoodooensis* Kavanaugh and Angel sp. nov. (near Hoodoo Pass, Mineral County, Montana); b, *S. merkelii* (G. Horn) (9 km SE of Lowell, Idaho County, Idaho); c, *S. regularis* (LeConte) (Hayden Creek, Kootenai County, Washington); d, *S. relictus* (G. Horn) (Selway River at O'Hara Campground, Idaho County, Idaho); e, *S. mannii* Wickham (Steptoe Canyon, Whitman County, Washington). Scale lines = 0.5 mm.

transverse impression at level of posterior margin of eye, frontal and occipital regions more or less continuous dorsally; one pair of supraorbital setae present, inserted just anterior to posterior margins or eyes. Genae expanded laterally as a narrow shelf in front of and below eye, with a distinct notch in the shelf in line with anterior margin of eye. Antennae (Fig. 3a) with antennomeres 5 to 11 densely pubescent, antennomeres 3 and 4 with sparsely scattered setae in addition to apical whorl of setae, antennomere 4 also very sparsely pubescent in apical half in some specimens. Labrum (Fig. 2a) deeply emarginate, with four setae on apical margin between lateral lobes, lateral lobes moderate in length; labial palpomere 2 with three or more setae.

*Prothorax.* Pronotum slightly wider than long (ratio length to width 0.94 or less), greatest

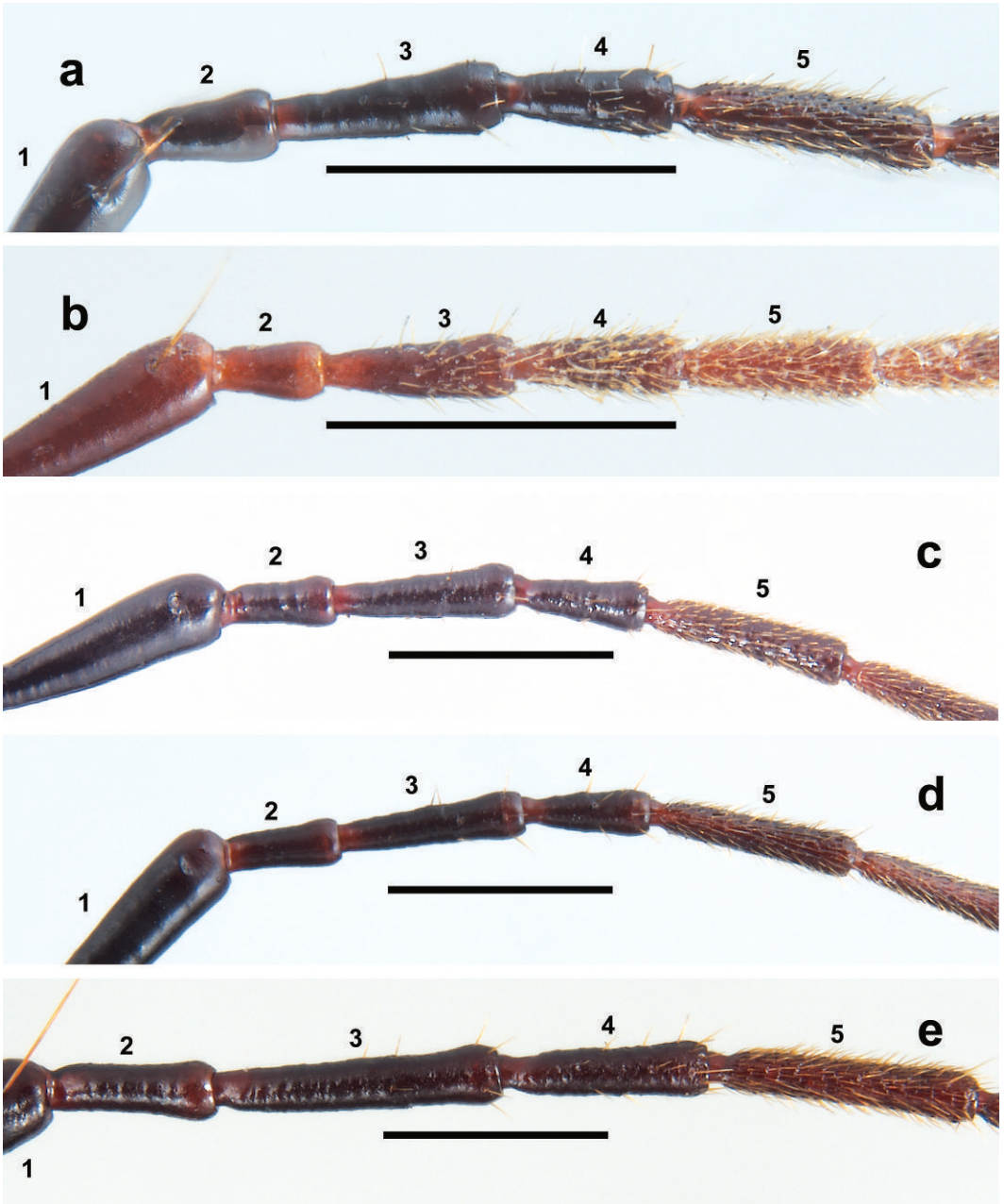


FIGURE 3. Digital photographs of right antenna, antennomeres 1 to 5, of *Scaphinotus* (*Pseudonomareus*) species, dorsal aspect, with antennomeres identified by number; a, *S. hoodoensis* Kavanaugh and Angel sp. nov. (near Hoodoo Pass, Mineral County, Montana); b, *S. merkelii* (G. Horn) (St. Joe National Forest, Idaho); c, *S. regularis* (LeConte) (Hayden Creek, Kootenai County, Washington); d, *S. relictus* (G. Horn) (Selway River at O'Hara Campground, Idaho County, Idaho); e, *S. mannii* Wickham (Steptoe Canyon, Whitman County, Washington). Scale lines = 1.0 mm.

width distinctly anterior to middle, lateral margin slightly and gradually sinuate anterior to hind angles, disc smooth or very faintly wrinkled, pronotal base impunctate; hind angles moderately obtuse, angulate; one pair of midlateral setiferous pores present, inserted at medial edge of lateral groove slightly anterior to middle (one specimen seen with a second midlateral seta unilaterally); one pair of basolateral setiferous pores present, inserted distinctly anterior to hind angles at medial edge of lateral groove. Propleural suture present, propleura smooth, impunctate. Protarsi of male (Fig. 4) with tarsomeres 1 to 3 markedly dilated, laterally expanded and subquadrate, with dense pads of adhesive setae over virtually entire ventral surface, tarsomere 4 narrower, triangular, without a pad of adhesive setae ventrally.

*Pterothorax.* Elytra with 13 regular, deeply impressed striae, striae 1 to 12 uninterrupted on disc, stria 13 partly interrupted by punctures of umbilicate series, all striae distinctly punctate, punctures moderately foveate, intervals moderately convex, intervals 4 and 8 each with two or more (three or four in most specimens) distinct, moderately foveate discal setiferous pores, those intervals catenate at discal pore insertions in most individuals; lateral margination of elytra slightly narrowed. Elytra epipleura smooth, impunctate or with only a few scattered, shallow, vaguely defined depressions. Metacoxae with anterior seta present, posteromedial seta absent.

*Abdomen.* Ventrite 6 with two pairs of apical paramedical setae in both males and females.

*Male genitalia.* Median lobe of aedeagus (Fig. 8) moderate in thickness and of nearly equal thickness throughout, ventral margin evenly arcuate in basal three-fourths, faintly recurved dorsally in apical one-fourth in lateral aspect (Fig. 8b), widest near midpoint of shaft length, straight, narrowed at apical one-third of shaft length, then parallel-sided in apical one-third and angularly tapered to a narrowly rounded point apically in dorsal aspect (Fig. 8a), armature of internal sac with a heavily sclerotized tubular section at basal one-third of shaft

**GEOGRAPHICAL DISTRIBUTION.**— This species currently is known only from the type locality, near Hoodoo Pass, 1750–1780 m, Mineral County, Montana, U.S.A.

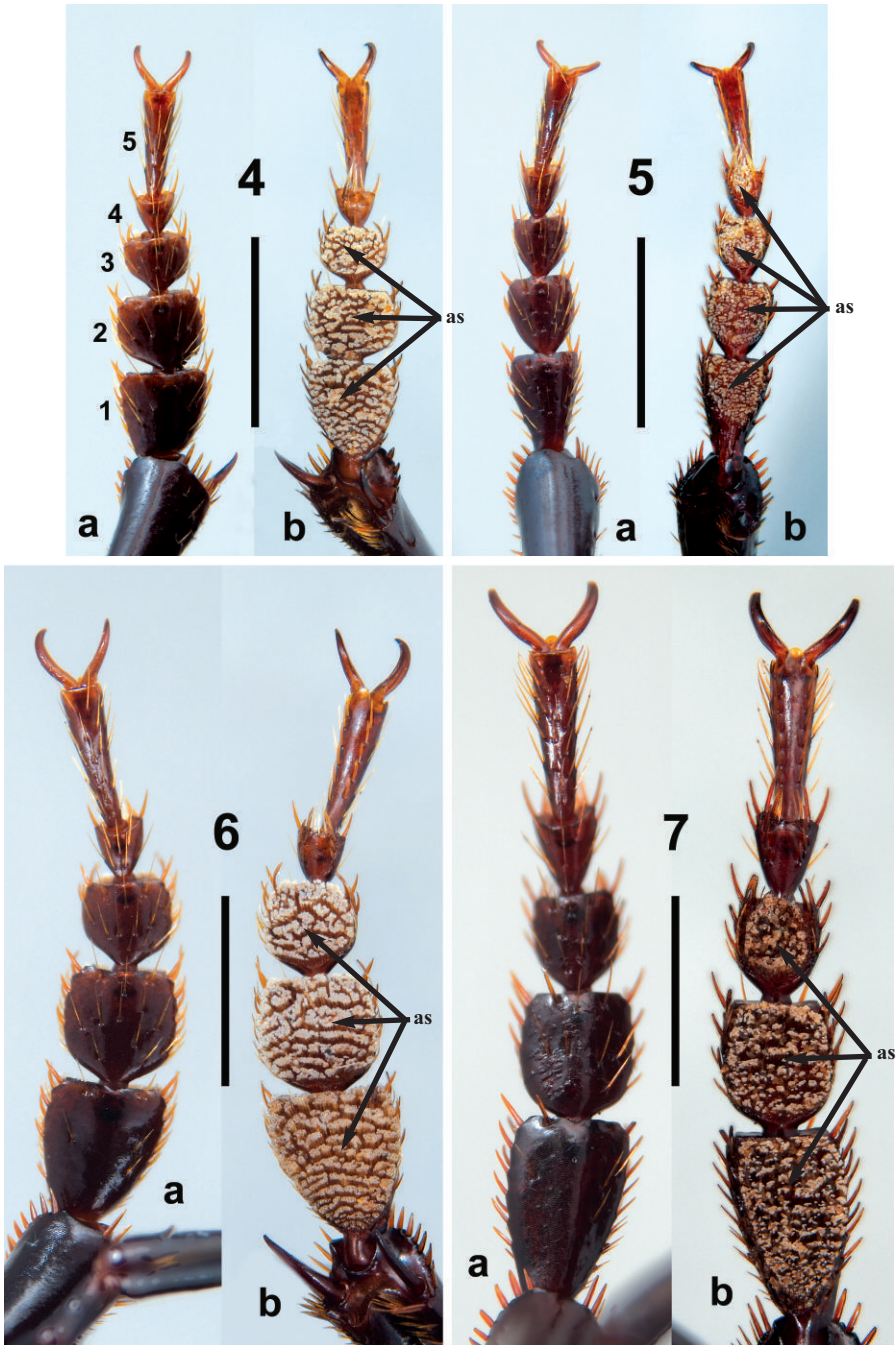
**HABITAT DISTRIBUTION.**— During daytime, adults of this species were found under loosely embedded stones and logs on the ground in the meadow/forest ecotone zone and slightly into the forest itself (Pl. I). Beetles were found walking around on the soil surface at night in the same areas.

**GEOGRAPHICAL RELATIONSHIPS WITH RELATED SPECIES.**— Almost all locality records for other *Pseudonomareus* species are from areas to the north and west of the type locality of *S. hoodooensis* and all are at lower elevations. Excluding that for our new species, the only records for the subgenus from Montana are for *S. merkelli* and *S. relictus*. Both of these species have been collected in molasses-baited pitfall traps in the vicinity of Lookout Pass, Mineral County, at an elevation of 1280 m (Russell 1968). This locality is approximately 70 km northwest of Hoodoo Pass and at an elevation about 500 m lower. *Scaphinotus relictus* has also been collected in Sanders County, 13 miles NE of St. Regis, at an elevation of about 800 m. This locality is about 40 km northnorthwest of Hoodoo Pass. While it is possible that the geographical ranges of *S. merkelli* and/or *S. relictus* may eventually be found to overlap with that of *S. hoodooensis*, these species are likely restricted to elevations below the altitudinal range of *S. hoodooensis* and so are not likely to occur in the same habitat.

***Scaphinotus (Pseudonomareus) manni* Wickham 1919**

Figures 2e, 3e, 7, 10

**RECOGNITION.**— Adults of this species can be distinguished from those of other species of *Pseudonomareus* by the following combination of character states: SBL = 13.0 mm or more (males 16.4–16.7 mm, females 17.7–18.3 mm); elytra moderately dull, microsculpture distinctly



FIGURES 4–7. Digital photographs of male left protarsus of *Scaphinotus* (*Pseudonomareus*) species, with tarsomeres identified by number; a, dorsal aspect; b, ventral aspect; as = pad of adhesive setae. Fig. 4. *S. hoodooensis* Kavanaugh and Angel sp. nov. (near Hoodoo Pass, Mineral County, Montana). Fig. 5. *S. merkelii* (G. Horn) (9 km SE of Lowell, Idaho County, Idaho). Fig. 6. *S. relictus* (G. Horn) (Selway River at O'Hara Campground, Idaho County, Idaho). Fig. 7. *S. manni* Wickham (Steptoe Canyon, Whitman County, Washington). Scale lines = 1.0 mm.

impressed, without metallic reflection; head with a more or less distinct transverse impression at level of posterior margin of eyes clearly delineating frontal and occipital regions; labrum (Fig. 2e) with lateral lobes markedly long and narrow; antennomere 4 (Fig. 3e) not pubescent, with only a very few scattered setae in addition to apical whorl of setae; pronotum with basolateral pair of setiferous pores absent; male protarsomere 1 (Fig. 7b) with pad of adhesive setae ventrally over virtually entire ventral surface, protarsomere 4 without a pad; elytra with 13 to 15 regular striae, only the lateral one or two slightly interrupted in some individuals, elytral intervals 4 and 8 each with two to six discal setiferous pores; median lobe of male aedeagus (Fig. 10) with ventral margin evenly arcuate in lateral aspect (Fig. 10b), widest at about apical one-third of shaft and gradually and arcuately tapered to a narrowly rounded apex in dorsal aspect (Fig. 10a).

**GEOGRAPHICAL DISTRIBUTION.**— This species is known only from a few localities in south-eastern Washington and northeast Oregon (Bergdahl 2014)

***Scaphinotus (Pseudonomareus) merkelii* (G. H. Horn) 1890**

Figures 2b, 3b, 5, 9

*Cychrus merkelii* G. H. Horn 1890:71. Holotype, a female, in MCZ, labeled: “Ida”/ “Merkel”/ “C. merkelii Horn”/ “Cychrus merkelii Horn” [red label]/ “MCZ Holotype 34934” [red label]. Type locality: Coeur d’Alene, Idaho (designated by Lindroth, 1961:20).

*Cychrus idahoensis* Webb 1901:133. Lectotype, here designated, a male, in WSU, labeled: “Moscow Mt. Idaho”/ “July 99”/ “Type I” [red label]/ “LECTOTYPE *Cychrus idahoensis* Webb, design. by D. H. Kavanaugh and K. W. Angel 2015”. We examined one male and two female paralectotypes with same data as lectotype, except each labeled with a different “Type” number (“II”, “3” and “IV”, respectively), and one additional female paralectotype (labeled: “Collins, Idaho July 24, 1898.”/ “Type 5”, all also in WSU. Each of these paralectotypes now also bears the following label: “PARALECTOTYPE *Cychrus idahoensis* Webb 1901, design. by D. H. Kavanaugh and K. W. Angel 2015” [yellow label]. Synonymy established by Gidaspow (1973). Type locality: Moscow Mountain, Latah County, Idaho.

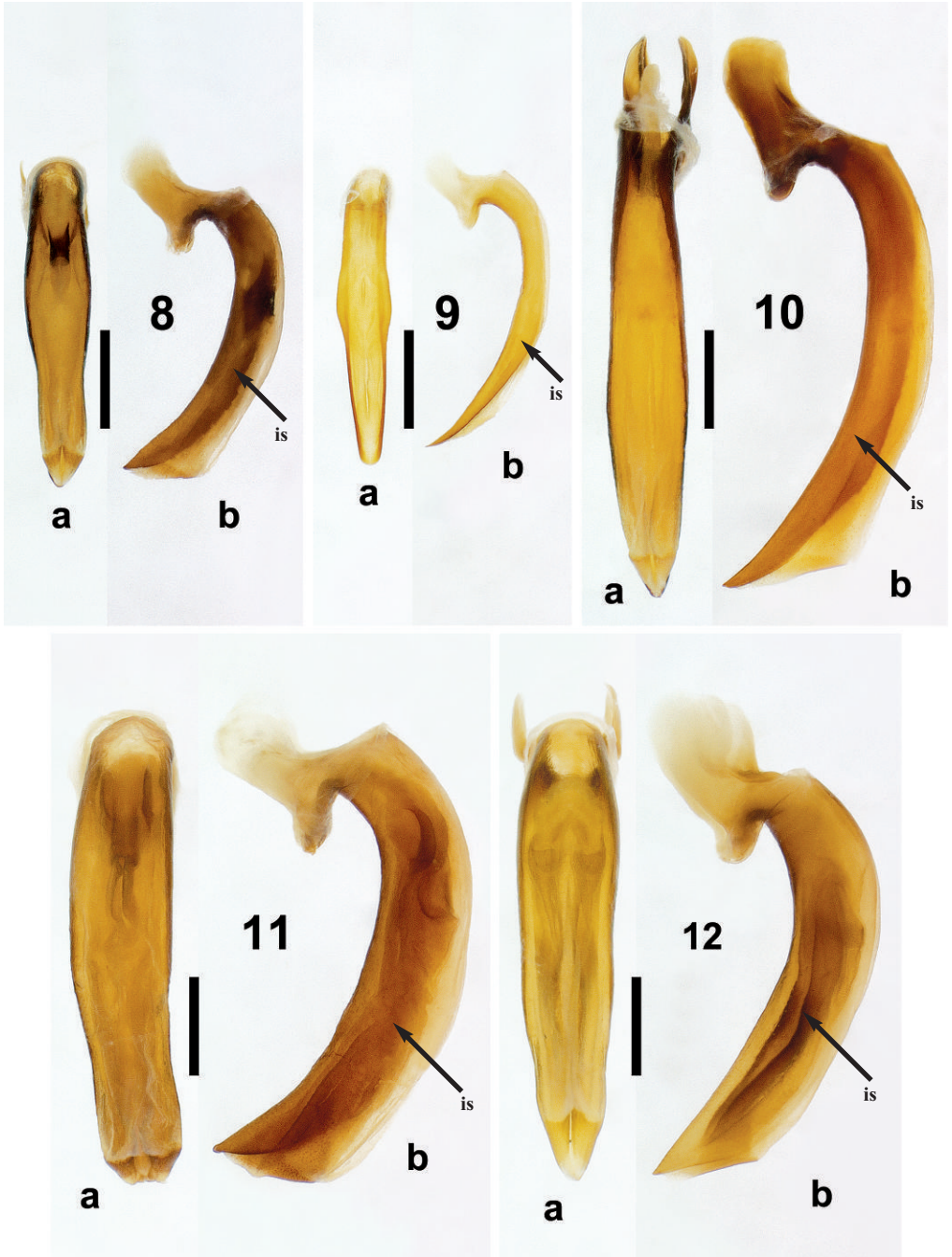
*Pseudonomareus merkelii* (G. H. Horn). Casey, 1914:30.

*Scaphinotus (Pseudonomareus) merkelii* (G. H. Horn). Roeschke 1907:##; Hatch 1953:45; Lindroth, 1961:20; Gidaspow 1973:74.

*Scaphinotus (Pseudonomareus) merkelii* (G. Horn). Bouquet 1993; Bergdahl 2014:4.

**NOTES ON NOMENCLATURE AND TYPES.**— In his original description of *Cychrus idahoensis*, Webb (1901) noted that he had seen a total of 14 specimens, including 11 from “Cedar Mountain” [now know as Moscow Mountain] and three from Collins, Idaho. This suggests that there are nine additional specimens, which we have not seen, that should also be considered paralectotypes of this name.

**RECOGNITION.**— Adults of this species can be distinguished from those of other species of *Pseudonomareus* by the following combination of character states: SBL = 12.5 mm or less (males 9.9–1.0 mm, females 10.7–12.2 mm); elytra moderately shiny, with microsculpture shallowly impressed, without or with faintly suggested bronze metallic reflection; head with a distinct transverse impression at level of posterior margin of eyes clearly delineating frontal and occipital regions; labrum (Fig. 2b) with lateral lobes markedly long and narrow; antennomere 4 (Fig. 3b) as pubescent as antennomere 5 or nearly so, apical half of antennomere 3 also but more sparsely pubescent; pronotum with basolateral pair of setiferous pores present; male protarsomere 1 (Fig. 5b) with pad of adhesive setae ventrally on apical two-thirds only, protarsomere 4 also with a pad; elytra with 13 to 15 striae, with none to all of them interrupted by punctures in and between striae, elytral intervals 4 and 8 without discal setiferous pores; median lobe of male aedeagus (Fig. 9) slen-



FIGURES 8–12. Digital photographs of median lobe of male aedeagus of *Scaphinotus* (*Pseudonomaretus*) species; a, dorsal aspect; b, left lateral aspect; is = internal sac. Fig. 8. *S. hoodoensis* Kavanaugh and Angel sp. nov. (near Hoodoo Pass, Mineral County, Montana). Fig. 9. *S. merkelii* (G. Horn) (Moscow Mountain, Latah County, Idaho). Fig. 10. *S. mannii* Wickham (Wawawai, Whitman County, Washington). Fig. 11. *S. regularis* (LeConte) (Moscow Mountain, Latah County, Idaho). Fig. 12. *S. relictus* (G. Horn) (Mount Spokane, Spokane County, Washington). Scale lines = 1.0 mm.

der, with ventral margin evenly arcuate in lateral aspect (Fig. 9b), widest and slightly flaired laterally just distal to midpoint of shaft and gradually tapered to a broadly rounded apex in dorsal aspect (Fig. 9a).

**GEOGRAPHICAL DISTRIBUTION.**— This species is known from southeastern British Columbia, northwestern Montana and northern and central Idaho (Gidaspow 1973; Bergdahl 2014).

***Scaphinotus (Pseudonomaretus) regularis (LeConte) 1884***

Figures 2c, 3c, 11

**RECOGNITION.**— Adults of this species can be distinguished from those of other species of *Pseudonomaretus* by the following combination of character states: SBL = 13.0 mm or more (males 14.0–16.6 mm, females 14.9–21.2 mm); elytra moderately shiny, microsculpture shallowly impressed, without metallic reflection; head with a distinct transverse impression at level of posterior margin of eyes clearly delineating frontal and occipital regions; labrum (Fig. 2c) with lateral lobes moderate in length and width; antennomere 4 (Fig. 3c) not pubescent, with only a very few scattered setae in addition to apical whorl of setae; pronotum with basolateral pair of setiferous pores present; male protarsomere 1 (as in Fig. 6b) with pad of adhesive setae ventrally over virtually entire ventral surface, protarsomere 4 without a pad; elytra with 13 regular striae, less regular laterally in a few individuals, elytral intervals 4 and 8 each with two to six discal setiferous pores; median lobe of male aedeagus (Fig. 11) thick, thickest near midpoint of shaft, ventral margin evenly arcuate in basal three-fourths, distinctly deflected ventrally in apical one-fourth in lateral aspect (Fig. 11b), widest near midpoint of shaft length, slightly deflected right, narrowed and parallel-side in apical one-fourth, angularly tapered to a flattened point apically in dorsal aspect (Fig. 11a), armature of internal sac as in Fig. 11.

**GEOGRAPHICAL DISTRIBUTION.**— This species is known from southeastern British Columbia, northern and central Idaho and southeastern Washington (Gidaspow 1973; Bergdahl 2014).

***Scaphinotus (Pseudonomaretus) relictus (G. H. Horn) 1881***

Figures 2d, 3d, 6, 12

**RECOGNITION.**— Adults of this species can be distinguished from those of other species of *Pseudonomaretus* by the following combination of character states: SBL = 13.0 mm or more (males 13.0–16.6 mm, females 14.7–20.3 mm); elytra moderately shiny, microsculpture shallowly impressed, without metallic reflection; head with a distinct transverse impression at level of posterior margin of eyes clearly delineating frontal and occipital regions; labrum (Fig. 2d) with lateral lobes moderate in length and width; antennomere 4 (Fig. 3d) not pubescent, with only a very few scattered setae in addition to apical whorl of setae; pronotum with basolateral pair of setiferous pores present; male protarsomere 1 (Fig. 6b) with pad of adhesive setae ventrally over virtually entire ventral surface, protarsomere 4 without a pad; elytra with 13–16 apparent striae, with at least lateral striae disrupted by punctures in and between striae, elytral intervals 4 and 8 each with two to six discal setiferous pores; median lobe of male aedeagus (Fig. 12) moderate in thickness and of nearly equal thickness throughout, ventral margin arcuate in basal one-fourth, straight in middle half, and slightly deflected ventrally in apical one-fourth in lateral aspect (Fig. 12b), widest near basal one-fourth of shaft length, straight, gradually tapered to a flattened point apically in dorsal aspect (Fig. 12a), armature of internal sac as in Fig. 12.

**GEOGRAPHICAL DISTRIBUTION.**— This species is known from southwestern Alberta and southeastern British Columbia, northwestern Montana, northern Idaho and eastern Washington (Gidaspow 1973; Bergdahl 2014).

## DISCUSSION

**POLYTHETELY AND COMPARISONS.**— As noted above, we recognize subgenus *Pseudonomare-tus* as a polythetic taxon (*sensu* Mayr 1969) including five species. In addition to the features shared by all members of the subgenus, there are several other features shared by members of all but one (or in two cases two) of the species, and some of these suggest relationships with other *Scaphinotus* subgenera.

Both Gidaspow (1973) and Ball and Bousquet (2001) used “dorsum without metallic reflection” as a key character for *Pseudonomare-tus* species; but *S. hoodoensis* adults have distinct metallic purple reflection on their elytra and most specimens also have faint metallic bronze, blue or purple reflection on their pronotum. A few specimens of *S. merkelii* also have very faint metallic bronze reflection on their elytra. Distinct dorsal metallic reflection is a feature seen in all *Nomare-tus* members and those of most other eastern North American subgenera of *Scaphinotus* as well as those of genus *Sphaeroderus* Dejean (1826). Among the other western North American subgenera, dorsal metallic reflection is seen in only a very few individual species. Lindroth (1961) noted that *Pseudonomare-tus* members have a distinct transverse impression on the head just behind the eyes to distinguish them in his key, but this impression is not present in *S. hoodoensis* adults. Presence of this transverse impression is also found in both *Nomare-tus* and *Maronetus* members, but not in members of the cychrine genus *Sphaeroderus*. *Scaphinotus man-nii*, *S. regularis*, and *S. relictus* adults have antennae with antennomeres 5 to 11 densely pubescent and antennomeres 3 and 4 without or with only a few sparsely scattered setae in addition to the apical whorl of setae. The apical half of antennomere 4 is sparsely pubescent in most specimens of *S. hoodoensis*, and antennomere 3 is without pubescence. In *S. merkelii* specimens, the apical half of antennomere 3 is moderately pubescent and antennomere 4 is almost as densely pubescent as antennomeres 5 to 11, a feature shared with all members of *Nomare-tus* and *Maronetus*. The presence of both midlat-eral and basolateral setiferous pores on the pronotum is shared by all *Pseudonomare-tus* members except those of *S. man-nii*, which lack the basolateral pair. The anterior tarsi of males of all *Pseudonomare-tus* species have tarsomeres 1 to 3 broadly expanded laterally and with dense pads of adhesive setae ventrally. This feature is shared with members of *Nomare-tus*, *Maronetus* and *Sphaeroderus*. In *S. merkelii* males, tarsomere 4 also has a small pad of adhesive setae ventrally, a feature not found in males of other *Pseudonomare-tus* species, but also seen in some but not all males of *Nomare-tus* species. Finally, the elytra of all *Pseudonomare-tus* members except those of *S. merkelii* have two or more (usually three or four) discal setiferous pores on intervals 4 and 8 in addition to those of the umbilicate series on the most laterad interval. This feature also is shared with some but not all members of *Nomare-tus* and *Maronetus*.

**PHYLOGENETIC CONSIDERATIONS.**— Although phylogenetic relationships among the species of subgenus *Pseudonomare-tus* and between this group and the other subgenera of *Scaphinotus* remain unresolved, features shared with members of subgenera *Nomare-tus* and *Maronetus* and also of genus *Sphaeroderus* suggest that *Pseudonomare-tus* may represent a clade near the base of the radiation of *Scaphinotus* or at least of the western North American element of that radiation. For her molecular phylogenetic analysis of subgenus *Brennus* Motschulsky (1866) based on molecular data, Culpepper (2011) included *S. hoodoensis*, *S. man-nii* and *S. regularis* among her outgroup taxa. *Scaphinotus merkelii* and *S. relictus* were not included in the analysis, nor were any represen-tatives of *Nomare-tus* or *Maronetus*. Even with this incomplete sampling of *Pseudonomare-tus* species and without representatives of either *Nomare-tus* or *Maronetus*, her results suggest that *Pseudonomare-tus* is the sister group, or at least part of the sister group, to the western North Amer-ican subgenera *Brennus* and *Stenocantharus* Gistel (1857). Features shared with *Nomare-tus*,



*Maronetus* and even *Sphaeroderus* members may be either symplesiomorphies or indicative of closer relationship (i.e., synapomorphies). Further analyses are required to make this determination. In either case, the geographical relationships of *Pseudonomareetus* species to the *Scaphinotus* faunas of both eastern and far western North America suggest a central role for this taxon in the evolutionary and biogeographic histories of genus *Scaphinotus*.

#### ACKNOWLEDGMENTS

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**A Revision of the *rhopalocerus* Species Group of *Bembecinus*  
Costa: An Addendum  
(Hymenoptera: Crabronidae: Bembicinae)**

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***Bembecinus priesneri* Schmid-Egger, 2004 is newly synonymized with *Bembecinus somalicus* (Arnold, 1940). The range of the *rhopalocerus* species group is extended north to Gebel Elba in southeastern Egypt.**

Herr Christian Schmid-Egger, in his e-mail of 30 April 2015, drew my attention to the fact that his species *Bembecinus priesneri* was probably a member of the *rhopalocerus* species group and that it was not treated in a recent revision of the group by F. Gess, W. Pulawski, and S. Gess (2015). He subsequently sent me the holotype of *priesneri*, a male, for examination. The study of this specimen (Fig. 1) as well as of a female from the California Academy of Sciences collection determined by him clearly demonstrated that *priesneri* is a junior synonym of *somalicus*. Both specimens show the characteristics of the *rhopalocerus* group as defined in the above publication (see p. 210, in key, 1b + 2b + 3a), as well as a unique color pattern of *somalicus*, and they otherwise fully agree with that species. This discovery results in two points:

1. The full synonymy of *Bembecinus somalicus* is as follows:

*Stizus quadristrigatus* race *somalicus* Arnold, 1940:116, ♀. Holotype: ♀, Somalia: Warderi, now Ethiopia: Warder (SAM).— **As *Bembecinus quadristrigatus somalicus***: R. Bohart and Menke, 1976:532 (new combination, new status, in checklist of world Sphecidae).— **As *Bembeci-***

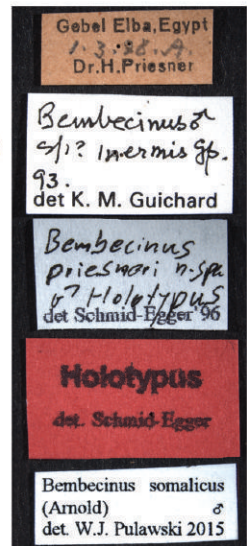


FIGURE 1. Holotype of *Bembecinus priesneri* Schmidt-Egger, 2004, and associated labels.

*nus somalicus*: F. Gess, W. Pulawski, and S. Gess, 2015:211, 213 (in key to *rhopalocerus* species group), 242 (new status, in revision of *rhopalocerus* species group).

*Stizus quadristrigatus* var. *dubiosus* Guiglia, 1941, 78, ♀. Holotype: ♀, Ethiopia: Gabredarre, now Kebri Dehar (MSNG). Synonymized with *Bembecinus somalicus* by Pulawski in F. Gess, W. Pulawski, and S. Gess, 2015:242.— **As *Bembecinus quadristrigatus dubiosus***: R. Bohart and Menke, 1976:531 (new combination, new status, in checklist of world Sphecidae).

*Bembecinus priesneri* Schmid-Egger, 2004b:19, ♀, ♂. Holotype: ♂, Egypt: Gebel Elba (coll. M. Schwarz, Ansfelden, Austria). **New synonym.**

2. The range of the *rhopalocerus* species group extends from the southern tip of Africa north to Gebel Elba in southeastern Egypt, not only to the Somalian Region of Ethiopia, as accepted by F. Gess, W. Pulawski, and S. Gess (2015).

#### ACKNOWLEDGMENTS

I sincerely thank Herr Christian Schmid-Egger for alerting me to the identity of *Bembecinus priesneri* and for a generous sending of several specimens of the *rhopalocerus* group for examination (including the holotype of *priesneri*).

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## **X-ray Microanalysis and the Chemical Elemental Composition of Gorgonian and Pennatulacean Axial Structures (Anthozoa, Octocorallia)**

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**By comparing the elemental compositions of the axes of five families of octocorals from both calcaxonian gorgonians and sea pens using energy dispersive X-ray microanalysis, the aim of this study is to gain insight relating to the phylogenetic relationships between these two groups of octocorals. The overall results across the specimens examined suggest that both groups of octocorals share similar elemental compositions and, therefore, offer little help in inferring phylogeny among taxa. However, this study also suggests the potential for a novel avenue of research for environmental impact assessments by using X-ray microanalysis to obtain the chemical compositions of the calcaxonian gorgonians and sea pens to evaluate the impact of ambient seawater composition with respect to various trace elements.**

**KEYWORDS:** octocorals, Calcaxonia, gorgonians, sea pens, Pennatulacea, X-ray microanalysis

Few papers have been published on mineral content, mineralization, and elemental composition of the skeletal components of octocorals and of these the three most relevant to this study include Folk (1974), MacIntyre, et al. (2000), and Bayer and MacIntyre (2001).

Grasshoff (1999; Grasshoff and Bargibant 2001) proposed and described the group name Calcaxonia for gorgonian families that share the character of a heavy calcified axis, that is solid throughout, and in which the calcified portion is dominant in comparison to the proteinaceous portion. He included the five families, Ifalukellidae, Chrysogorgiidae, Primmoidae, Ellisellidae, and Isidididae.

Virtually all octocorals have endoskeletal elements in the form of a consolidated central axis or numerous minute sclerites to support the colonies. Both calcaxonian gorgonians and sea pens have solid central axes and have been hypothesized as sister groups, yet very few studies have been done regarding the axial chemical composition in the calcaxonians and pennatulaceans. Thus one of the central questions is: Do these two groups of octocorals share a similar chemical composition across taxa? We here apply X-ray microanalysis to representative specimens from each family of both calcaxonian gorgonians and pennatulaceans to answer this question.

The overarching goal of this study is to portray the phylogenetic relationships between two groups of octocorals: the calcaxonian gorgonians (sea fans) and the pennatulaceans (sea pens), by examining the morphological characters of the axial skeleton of both groups of octocorals using scanning electron microscopy. The microstructural inspection was undertaken on the transverse cross sections of the bare axes of both groups of octocorals to achieve a detailed understanding and to record the special traits that each taxon revealed. By comparing the characteristics of the specimens inspected between the two groups of octocorals, the preliminary morphological interrelationships can be delineated. This is presumably the first study to compare the two groups using energy dispersive X-ray microanalysis on the axis of octocorals for elemental analysis.

## MATERIALS AND METHODS

**MATERIALS.**— All of the octocoral specimens used in this study are housed in the Invertebrate Zoology Collection of the California Academy of Sciences. Three gorgonian species, *Ellisella* sp. (family Ellisellidae), *Isis hippuris* (family Isididae), *Plumigorgia hydroides* (family Ifalukellidae), and three sea pen species, *Cavernularia* sp. (family Veretillidae), *Stylatula* sp. (family Virgulariidae) and *Virgularia* sp. (family Virgulariidae), were examined. The detailed collection information for each specimen is given as follows: *Ellisella* sp. (family Ellisellidae); partial colony wet preserved in 75% ethanol; CAS-154877; Palau, Uchelbeluu Reef, Koror, near SW corner 7.00°15.61'N 134.00°31.14'E, 123 m, 1 March 2001; Pat Colin aboard research submersible. *Isis hippuris* (family Isididae); partial colony wet preserved in 75% ethanol; CAS-175045; Taiwan, Taitung County, Green Island, 17 m, 14 July 2007; Cerise Chen. *Plumigorgia hydroides* (family Ifalukellidae); whole colony wet preserved in 95% ethanol; CAS-180888; Philippines, Palawan Province, Calamian Group, Busuanga Island, Magic Reef, 11 m, 24 February 2010; Gary C. Williams. *Virgularia* sp. (family Virgulariidae); Papua New Guinea, *Virgularia* sp. (family Virgulariidae); whole colony wet preserved in 75% ethanol; CAS-099847; Papua New Guinea, Madang Province, Pig [Tab] Island, embayment on W coast of island, "center", 6–15 m, 5 June 1992; Gary C. Williams. *Cavernularia* sp. (family Veretillidae); whole colony wet preserved in 75% ethanol; CAS-103391; Pacific Ocean, South China Sea, Taiwan Strait, Formosa Bank, 40–50 fm; Franz B. Steiner. *Stylatula* sp. (family Virgulariidae); whole colony wet preserved in 75% ethanol; CAS-140902; California, San Francisco Estuary, San Francisco Bay, San Francisco County, between Angel Island and Treasure Island 37.00°50.35'N 122.00°24.35'W, 18 m, 14 August 1973; F. Nichols. Specimens were collected from shallow water via scuba diving, while deeper water specimens were collected by bottom trawling.

**SEM SAMPLE PREPARATION.**— To acquire the bare axes out of the sclerite-impregnated coenenchymal tissue in gorgonians and from the fleshy muscular tissue in pennatulaceans, the axes were first sectioned into fragments using a razor blade or bolt clippers or by bending or twisting the axial skeleton perpendicular to the longitudinal axis until it fractured. Then, the samples were treated with concentrated sodium hypochlorite (NaOCl) for an average of 10–15 minutes depending upon the amount of organic matrix to be removed (Lewis et al. 1992). The bleach-treated axes were then rinsed with distilled water several times, processed with ethanol dehydration (Kim et al. 1992), and then allowed to air dry. The dried axial rods were mounted on aluminum SEM stubs with Electrodag® 502 or Colloidal Graphite, then sputter-coated before imaging using a precision etching coating system (PECS, 682, Gatan Inc, Pleasanton, CA) with carbon; a continuous line of silver paint was also applied along the sides of each axial rod, and to the very bottom (the point where the axis is attached on the stub) to facilitate conductivity.

**SEM IMAGING AND X-RAY MICROANALYSIS.**— The SEM images and X-ray microanalysis were taken on a Zeiss Ultra 55 field emission scanning electron microscope equipped with an Oxford INCA energy dispersive spectrometer (EDS). The Everhart-Thornley detector (SE2) and angle selected backscatter (AsB) detector were used at 25 kV accelerating voltage and 60  $\mu$ m of aperture size in high beam current condition (to allow effective excitation of X-ray line energy for elements with higher shell values) with 8.5 mm analytical working distance (for the optimum microanalysis performance purpose) under the frame average noise reduction method.

## RESULTS

**CALCULATIONS OF ELECTRON RANGE ( $R_{KO}$ ) AND X-RAY RANGE ( $R_X$ ).**— The calculation of electron range ( $R_{KO}$ ) of calcium (the major element found in all samples other than carbon and oxy-

gen) was carried out using the equation of Kanaya and Okayama (1972) to measure the interaction volume, where  $A$  is the atomic weight (g/mole),  $Z$  is the atomic number,  $\rho$  is the density (g/cm<sup>3</sup>),  $E_0$  is the beam energy (keV), and  $R_{KO}$  is calculated in micrometers with the constant 0.0276 (Goldstein et al. 2003); by inserting the beam energy 25 keV along with calcium's atomic weight 40.08 g/mole, atomic number 20 and density 1.53 g/cm<sup>3</sup> to the equation, the electron range ( $R_{KO}$ ) of calcium 16.072  $\mu\text{m}$  was acquired.

$$R_{KO}(\mu\text{m}) = \frac{0.0276A}{Z^{0.89}\rho} E_0^{1.67}$$

While the X-ray range of calcium was calculated using the X-ray range equation according to Anderson and Hasler (1966) to measure the depth of X-ray production, where  $R_X$  has units of micrometers,  $E$  is in keV and  $\rho$  is in g/cm<sup>3</sup>;  $E_C$  is the critical ionization or exciting energy, also known as the excitation potential or X-ray absorption edge energy (Goldstein et al. 2003). Again using the values of beam energy 25 keV and calcium's density 1.53 g/cm<sup>3</sup>, as well as the critical ionization energy of both  $K\alpha$  and  $L\alpha$  as 4.038 keV and 0.349 keV, respectively; the X-ray range for calcium  $K\alpha$  was acquired as 8.897  $\mu\text{m}$ , and the X-ray range for calcium  $L\alpha$ , was acquired as 9.326  $\mu\text{m}$ .

$$R_X(\mu\text{m}) = \frac{0.064}{\rho} (E_0^{1.68} - E_C^{1.68})$$

## SEM/EDS Results

### GORGONIANS

#### Family Isididae

##### *Isis hippuris*

Figures 1A–B, 2A–C.

The bar chart in Figure 2B presents the ten elements identified from the axial skeleton of the gorgonian *Isis hippuris*. Three major elements prominently shown in the chart are carbon (21.9 wt%), oxygen (41.71 wt%) and calcium (31.84 wt%); two minor elements are fluorine (1.90 wt%) and magnesium (2.43 wt%); the five remaining trace elements are barely seen from the chart: sodium (0.29 wt%), aluminum (0.07 wt%), sulfur (0.28 wt%), strontium (0.11 wt%) and the rare earth element (REE) ytterbium (0.19 wt%). The summary EDS results for both spectrum 1 (the horizontal site of interest) and spectrum 2 (the vertical site of interest) are listed in Table 1.

TABLE 1. EDS results of spectrum 1 and 2 for gorgonian *Isis hippuris* axial cross-section surface from Figure 2A. (All results are in weight%)

Elements	C	O	F	Na	Mg	Al	S	Ca	Sr	Yb	Total
Spectrum 1	21.17	41.5	1.97	0.29	2.43	0.07	0.29	31.99	0.12	0.18	100
Spectrum 2	21.2	41.91	1.82	0.3	2.43	0.06	0.28	31.68	0.1	0.2	100
Mean	21.19	41.71	1.9	0.29	2.43	0.07	0.28	31.84	0.11	0.19	100
Std. deviation	0.02	0.29	0.1	0.01	0	0.01	0	0.22	0.01	0.01	
Max.	21.2	41.91	1.97	0.3	2.43	0.07	0.29	31.99	0.12	0.2	
Min.	21.17	41.5	1.82	0.29	2.43	0.06	0.28	31.68	0.1	0.18	

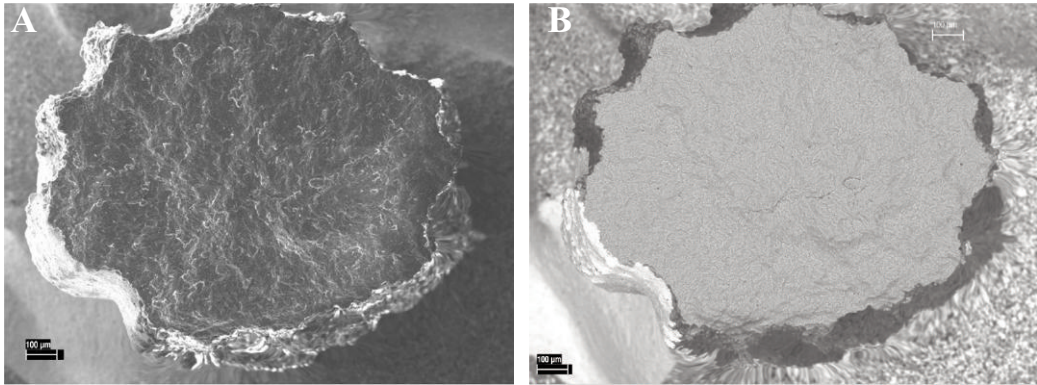


FIGURE 1. Scanning electron microscope (SEM) micrographs of a cross-sectional view of a gorgonian *Isis hippuris* axial skeleton. (A) Secondary electron (SE) image. Scale bar = 100 µm. (B) Back-scattered electron (BSE) image. Scale bar = 100 µm. In both images the charging effect is visible from the lower right corner, where some distortion occurred alongside the axial rod, while no such effect occurred in the silver paint covered area. No significant chemical composition change can be observed from the BSE image due to the lack of contrast across the surface of the axis.

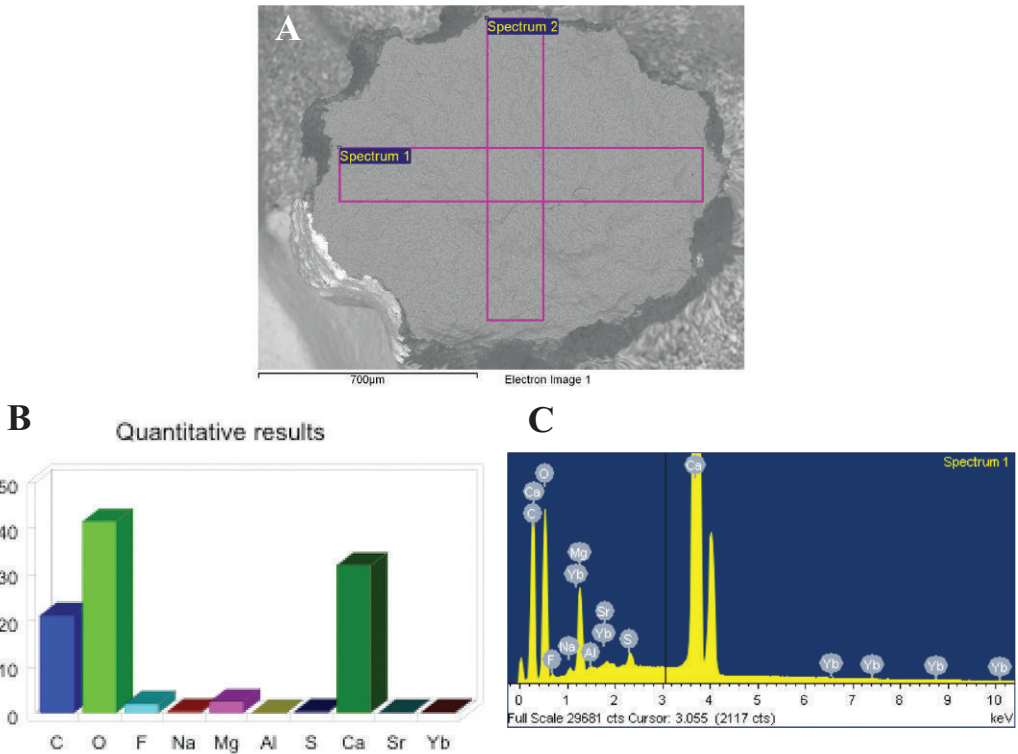


FIGURE 2. Energy dispersive spectrometer (EDS) area scan dataset. (A) EDS site of interest BSE image in a cross-sectional view of a gorgonian *Isis hippuris* axial skeleton acquired by INCA Energy software using the same region as Figure 1, where spectrum 1 was collected across the full span of the maximum horizontal length of the axial surface and spectrum 2 was collected across the full span of the maximum vertical length of the axial surface. Scale bar = 100 µm. (B) Bar chart of the quantitative results from (C) spectrum 1 for reference in that the analytical results of the two sites are fairly similar as presented in Table 1.



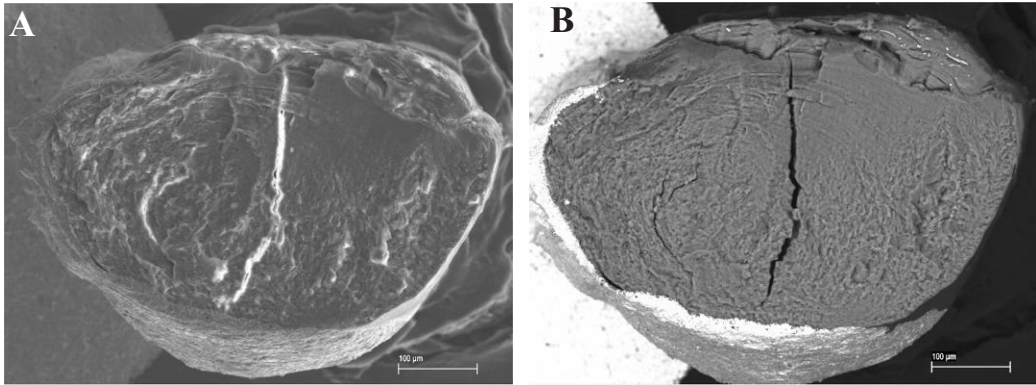


FIGURE 3. Scanning electron microscope (SEM) micrographs of a cross-sectional view of a gorgonian *Plumigorgia hydroides* axial skeleton. (A) Secondary electron (SE) image. The crack appearing in the center of the axis is an artifact caused by the dehydration of the axis (specimen was wet preserved in 95% ethanol); charging was built up inside the crack resulting in the very bright band along the crack region. Scale bar = 100 µm. (B) Back-scattered electron (BSE) image. There is no visible chemical composition change on the surface of the axis except the bright spots on the upper right corner caused by contamination from remnants of razor blade that attached on top of the surface. Scale bar = 100 µm.

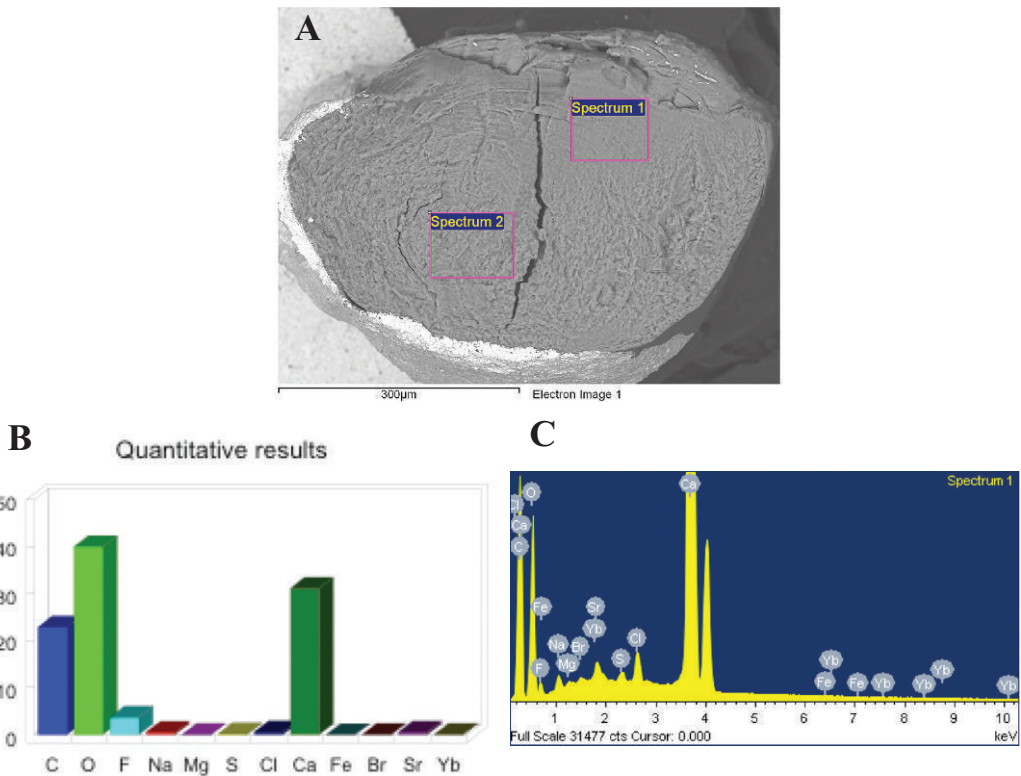


FIGURE 4. Energy dispersive spectrometer (EDS) area scan dataset. (A) EDS site of interest BSE image in a cross-sectional view of a gorgonian *Plumigorgia hydroides* axial skeleton acquired by INCA Energy software using same region as Figure 3, partial area scan was applied due to the visible topographical differences of the surfaces on both sides of the axis, thus only two small areas were selected for EDS analysis. Scale bar = 300 µm. (B) Bar chart of the quantitative results from (C) spectrum 1 for reference in that the analytical results of the two sites are identical as seen in Table 2.

**Family Ifalukellidae*****Plumigorgia hydroides***

Figures 3A–B, 4A–C.

As seen in Figure 4B, there are twelve identified elements, two more than that in *Isis hippuris* in which the major elements present in the axis of *Plumigorgia hydroides* are again carbon (21.93 wt%), oxygen (40.07 wt%) and calcium (32.11 %), with one minor element fluorine found at 3.87 wt%. The remaining trace elements are sodium (0.55 wt%), magnesium (0.07 wt%), sulfur (0.15 wt%), chlorine (0.45 wt%), iron (0.04 wt%), bromine (0.09 wt%), strontium (0.53 wt%) and REE ytterbium (0.14 wt%). The summary EDS results for both spectrum 1 (the right side of the axis) and spectrum 2 (the left side of the axis) are listed in Table 2.

TABLE 2. EDS results of spectrum 1 and 2 for gorgonian *Plumigorgia hydroides* axial cross-section surface from Figure 4A. (All results are in weight%)

Spectrum	C	O	F	Na	Mg	S	Cl	Ca	Fe	Br	Sr	Yb	Total
Spectrum 1	22.92	40.01	3.7	0.55	0.08	0.18	0.62	31.13	0.04	0.1	0.58	0.1	100
Spectrum 2	20.95	40.14	4.04	0.56	0.07	0.11	0.29	33.08	0.03	0.07	0.47	0.18	100
Mean	21.93	40.07	3.87	0.55	0.07	0.15	0.45	32.11	0.04	0.09	0.53	0.14	100
Std. deviation	1.39	0.1	0.24	0.01	0.01	0.05	0.23	1.38	0	0.03	0.07	0.06	
Max.	22.92	40.14	4.04	0.56	0.08	0.18	0.62	33.08	0.04	0.1	0.58	0.18	
Min.	20.95	40.01	3.7	0.55	0.07	0.11	0.29	31.13	0.03	0.07	0.47	0.1	

**Family Ellisellidae*****Ellisella* sp.**

Figures 5A–B, 6A–D.

From the linescan BSE image and the element linescan graph (Figure 6A and 6B) a high amount of calcium in the blue line can be seen spread through the horizontal axis surface, with an apparently declining pattern in the central axis region; the same trends can be observed in carbon (in red, 23.75 wt%), oxygen (in orange, 37.69 wt%) and magnesium (in light green, 2.14 wt%), which suggests that the core region of the axis contains lower amounts of the three major elements carbon (23.75 wt%), oxygen (37.69 wt%) and calcium (31.89 wt%), as well as magnesium (2.14 wt%), one of the two minor elements other than fluorine (3.40 wt%). All other trace elements like sodium (0.36 wt%), aluminum (0.05 wt%), sulfur (0.30 wt%), chlorine (0.23 wt%), iron (0.04 wt%), strontium (0.13 wt%) and REE ytterbium (0.14 wt%) have a more evenly distributed pattern with much flatter overall trends along the line. The weight percentage of all twelve identified elements is given in Table 3.

TABLE 3. EDS results of the sum spectrum for the gorgonian *Ellisella* sp. axial cross-section surface from Figure 6A. (All results are in weight%)

Element	C	O	F	Na	Mg	Al	S	Cl	Ca	Fe	Sr	Yb	Total
Sum Spectrum (Weight%)	23.75	37.69	3.4	0.36	22.14	0.05	0.3	0.23	31.89	0.04	0.13	0.01	100

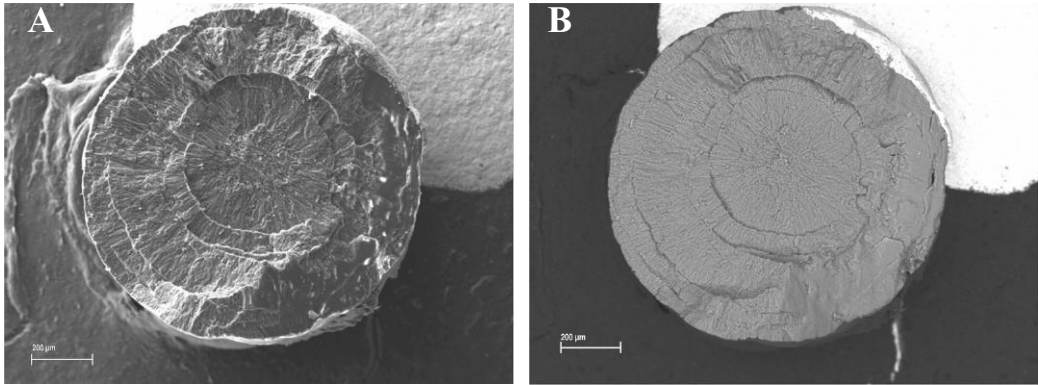


FIGURE 5. Scanning electron microscope (SEM) micrographs of a cross-sectional view of a gorgonian *Ellisella* sp. axial skeleton. (A) Secondary electron (SE) image. The axis of *Ellisella* sp. is featured by the concentric growth rings resembling that in trees, also by the slightly radiating patterns on the surface. These characters are useful for comparative morphology studies on calcaxonian gorgonians and sea pens. Scale bar = 200 µm. (B) Back-scattered electron (BSE) image. The compositional change is minute since again no detectable contrast is observed in the image though the topographical contrast is apparent like that in the SE image. Scale bar = 200 µm.

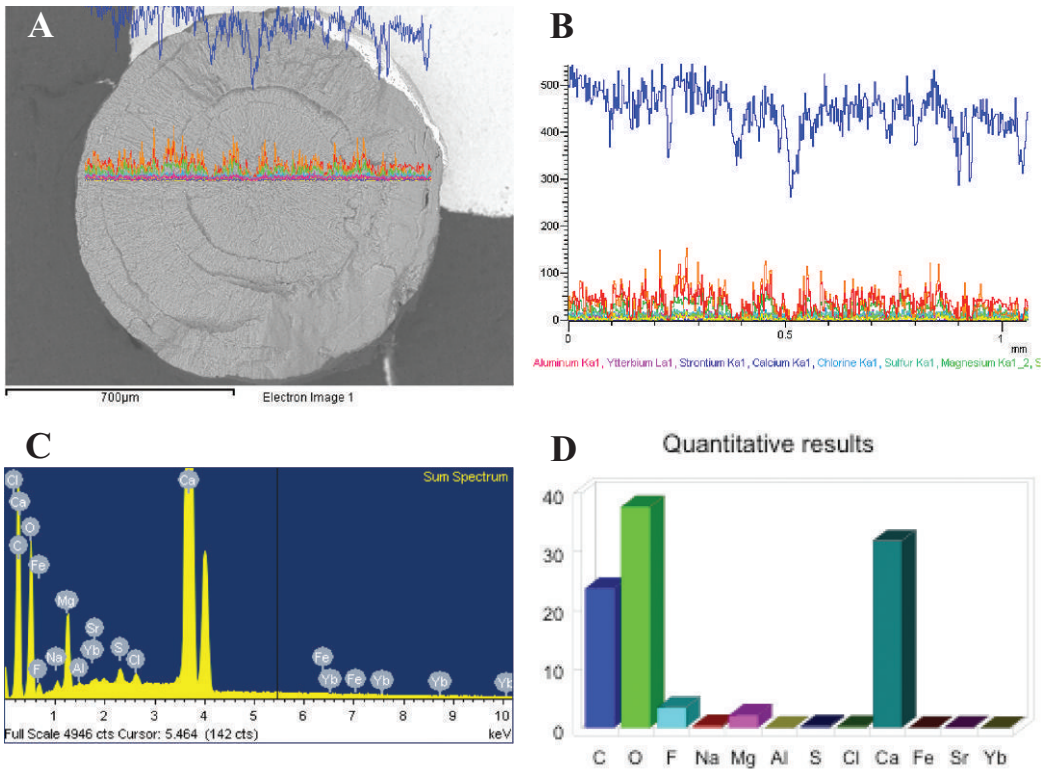


FIGURE 6. Energy dispersive spectrometer (EDS) linescan dataset. (A) EDS linescan site of interest BSE image in a cross-sectional view of a gorgonian *Ellisella* sp. axial skeleton acquired by INCA Energy software using same region as Figure 5, horizontal linescan through the middle of the axis was applied for EDS analysis to examine the distribution of elements along the line. Scale bar = 700 µm. (B) Element linescan result displaying grouped linescans as colored: carbon (red), oxygen (orange), fluorine (yellow), sodium (light green), magnesium (green), aluminum (pink), sulfur (aqua), chlorine (light blue), calcium (blue), strontium (indigo), ytterbium (purple), iron is not shown in the graph. (C) Sum spectrum of the linescan. (D) Bar chart of the quantitative results from the sum spectrum.

## SEA PENS

## Family Veretillidae

*Cavernularia* sp.

Figures 7A–B, 8A–D.

In contrast to the linescan patterns of the gorgonian *Ellisella* sp. which has lower values of carbon (in red), oxygen (in orange), calcium (in blue) and magnesium (in light green) in the central core region, the linescan graph Figure 8A showed no significant declination of all four elements on the site of central core region of the sea pen *Cavernularia* sp.; instead, the weight percentage of carbon, oxygen and magnesium are even higher than the other parts of the line section. However, declining patterns of those four elements can still be seen on the site approximately 400  $\mu\text{m}$  away from the left edge of the axial surface, which may be related to the rough surface features shown in Figure 7A that caused the drop of values in the four elements stated above. Besides the three major elements of carbon (17.44 wt%), oxygen (46.43 wt%), calcium (31.35wt%) along with the two minor elements fluorine (1.03 wt%) and magnesium (2.84 wt%), five other trace elements were identified: sodium (0.3 wt%), aluminum (0.06 wt%), sulfur (0.27 wt%), strontium (0.19 wt%) and REE ytterbium (0.11 wt%). All five trace elements and fluorine have flat and steady patterns of line trends compared to that of carbon, oxygen, calcium and magnesium. The weight percentage value of all ten identified elements can be found in Table 4.

TABLE 4. EDS results of the sum spectrum for sea pen *Cavernularia* sp. axial cross-section surface from Figure 8A. (All results are in weight%)

Spectrum	C	O	F	Na	Mg	Al	S	Ca	Sr	Yb	Total
Sum Spectrum (Weight%)	17.44	46.43	1.03	0.3	2.84	0.06	0.27	31.35	0.19	0.11	100

*Virgularia* sp.

Figures 9A–B, 10A–D.

Like the observations in the previous specimens, some degree of fluctuations and shift of linescans of carbon (in purple, 20.42 wt%), oxygen (in light green, 44.95 wt%), calcium (in green, 29.35 wt%) and magnesium (in dark green, 2.57 wt%) are found on *Virgularia* sp. as well (Figure 10B); they are mostly found along the central axis region, which may be implied by the BSE image that shows the darker contrast region in the central core of the axis. The fluctuated patterns are consistent among the four elements, thus a clear grouped relationship can be seen when zooming to higher magnification in Fig 10B. The linescan patterns of fluorine (in pink, 1.60 wt%) and the four remaining trace elements sodium (in blue, 0.55 wt%), sulfur (in sky blue, 0.30 wt%), chlorine (in red, 0.07 wt%) and REE ytterbium (in orange, 0.19 wt%) are similar in nature, with an evenly displayed appearance along the linescan section. Table 5 displays the weight percentage value of all nine identified elements.

TABLE 5. EDS results of the sum spectrum for sea pen *Virgularia* sp. axial cross-section surface from Figure 10A. (All results are in weight%)

Spectrum	C	O	F	Na	Mg	S	Cl	Ca	Yb	Total
Sum Spectrum (Weight%)	20.42	44.95	1.6	0.55	2.57	0.3	0.07	29.35	0.19	100

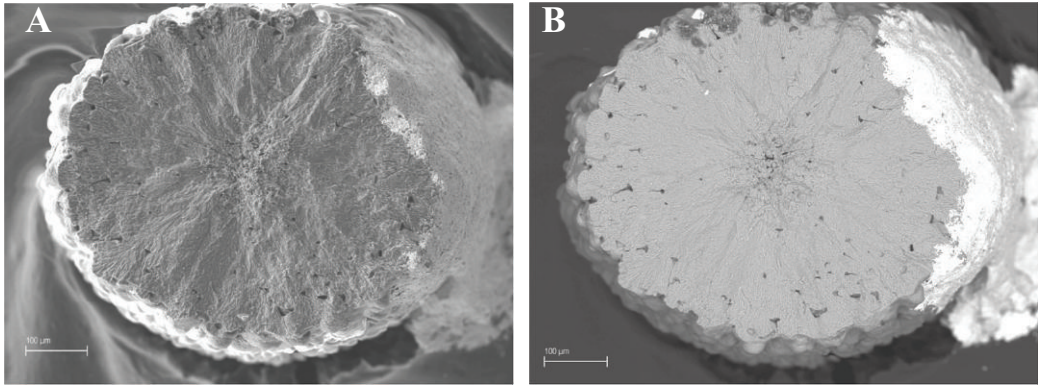


FIGURE 7. Scanning electron microscope (SEM) micrographs of a cross-sectional view of a sea pen *Cavernularia* sp. axial skeleton. (A) Secondary electron (SE) image shows an uneven fracture surface of the axis and multiple comma-like indents around the outer rim of the axial surface known as the imprints of chimney cell extensions according to Ledger and Franc (1978). Scale bar = 100  $\mu$ m. (B) Back-scattered electron (BSE) image. Same as the previous specimens examined, there are no perceivable compositional changes on the imaging area of axial surface, yet the topographical differences and more chimney cell extensions are clearly shown. Scale bar = 100  $\mu$ m.

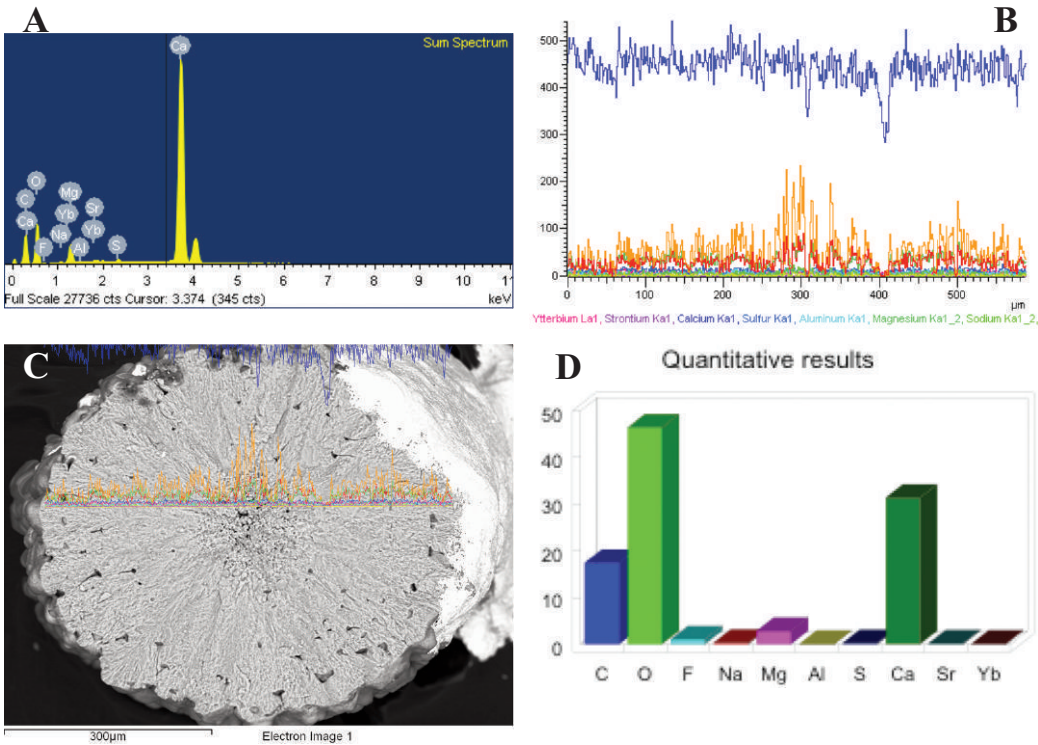


FIGURE 8. Energy dispersive spectrometer (EDS) linescan dataset. (A) EDS linescan site of interest BSE image in a cross-sectional view of a sea pen *Cavernularia* sp. axial skeleton acquired by INCA Energy software using same region as Figure 7, horizontal linescan through the middle of the axis was applied for EDS analysis to examine the distribution of elements along the line. (B) Element linescan result displaying grouped linescans as colored: carbon (red), oxygen (orange), fluorine (yellow), sodium (light green), magnesium (green), aluminum (aqua), sulfur (light blue), calcium (blue), strontium (purple), ytterbium (pink). (C) Sum spectrum of the linescan. Scale bar = 300  $\mu$ m. (D) Bar chart of the quantitative results from the sum spectrum.

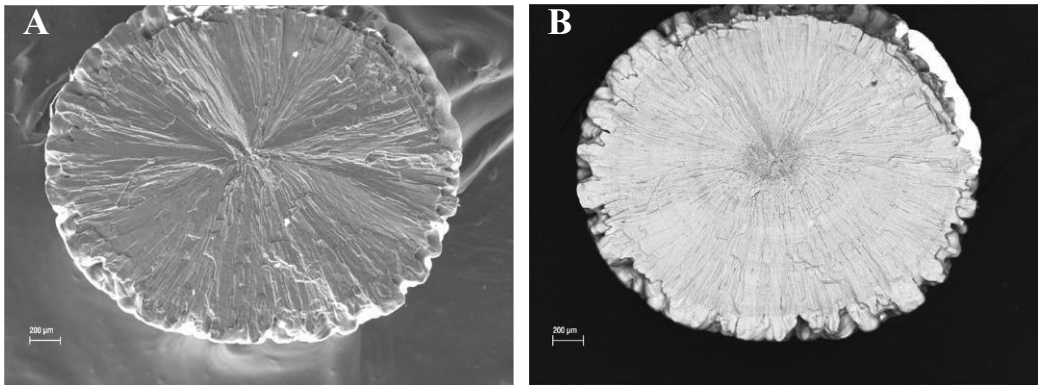


FIGURE 9. Scanning electron microscope (SEM) micrographs of a cross-sectional view of a sea pen *Virgularia* sp. axial skeleton. (A) In this secondary electron (SE) image a great degree of the radiating patterns well-arranged across the whole axial surface can be observed, such character is also used in the morphological phylogenetic studies of the calcaxonian gorgonians and sea pens. Scale bar = 200 μm. (B) Back-scattered electron (BSE) image. There seemed to be some chemical composition contrast appearing darker in the central portion of the axis, though several between-site area scans were performed, yet no differences in chemical composition can be found (data not shown); however, the between-site changes on weight percentage value of some elements can be detected as shown in the next Figure 10B. Scale bar = 200 μm.

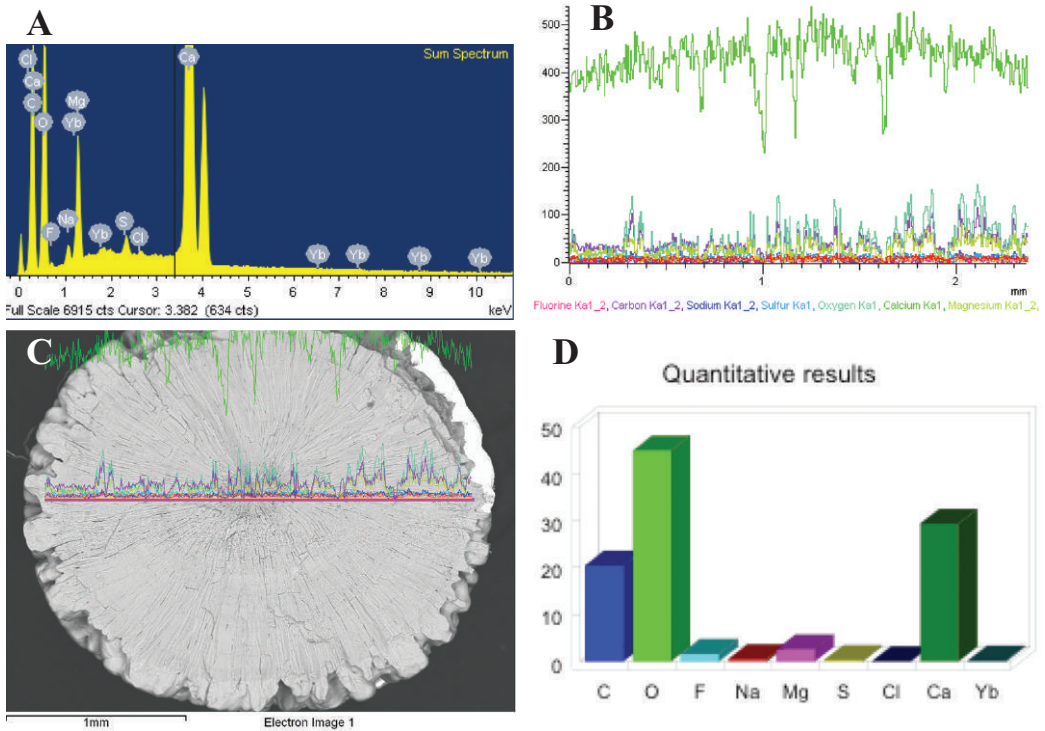


FIGURE 10. Energy dispersive spectrometer (EDS) linescan dataset. (A) EDS linescan site of interest BSE image in a cross-sectional view of a sea pen *Virgularia* sp. axial skeleton acquired by INCA Energy software using same region as Figure 9, horizontal linescan through the middle of the axis was applied for EDS analysis to examine the distribution of elements along the line. (B) Element linescan result displaying grouped linescans as colored: carbon (purple), oxygen (bright green), fluorine (pink), sodium (blue), magnesium (green), sulfur (teal), chlorine (red), calcium (light green), ytterbium (gold). (C) Sum spectrum of the linescan. Scale bar = 1 mm. (D) Bar chart of the quantitative results from the sum spectrum.

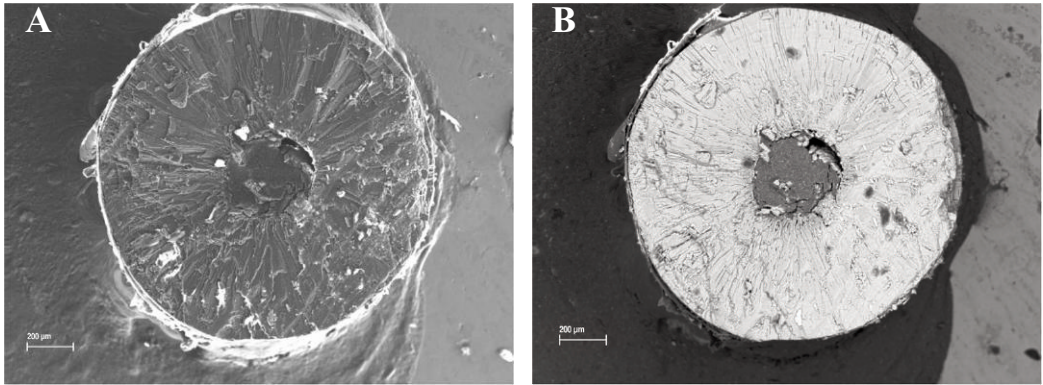


FIGURE 11. Scanning electron microscope (SEM) micrographs of a cross-sectional view of a sea pen *Stylatula* sp. axial skeleton. (A) Secondary electron (SE) image. The radiating patterns extending from the boundaries of the central core like that in *Virgularia* sp. are visible around the axis, and note that the central core is not prominent compared to that in the BSE image. Also visible are the charging effects on the scattered debris (possibly the contents coming from the hollow part of the central core) near the core and some places of the bottom axial surface. Scale bar = 200  $\mu$ m. (B) Back-scattered electron (BSE) image. Atomic composition contrast is very strong on this image, where the central core is very distinctly shown in black/gray in comparison to the white peripheral axis regions. A few black dots with similar coloration as the central core are present on the axial surface near the top and the right of the image, likely the contents breaking from the core and attached on the axial surface. Scale bar = 200  $\mu$ m.

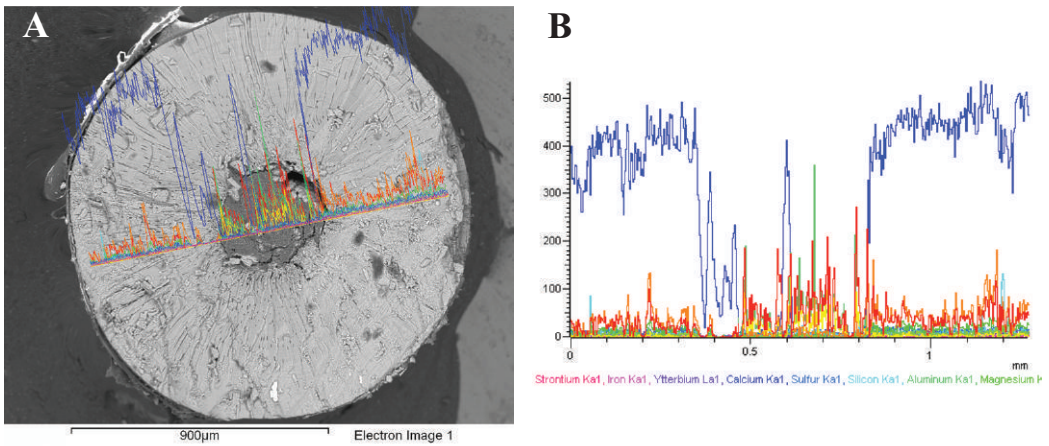


FIGURE 12. Energy dispersive spectrometer (EDS) linescan dataset. (A) EDS linescan site of interest BSE image in a cross-sectional view of a sea pen *Stylatula* sp. axial skeleton acquired by INCA Energy software using same region as Figure 11, horizontal linescan through the middle of the axis was applied for EDS analysis to examine the distribution of elements along the line. Scale bar = 900  $\mu$ m. (B) Element linescan result displaying grouped linescans as colored: carbon (red), oxygen (orange), fluorine (yellow), sodium (green), magnesium (light green), aluminum (bright green), silicon (aqua), sulfur (light blue), calcium (blue), strontium (pink), ytterbium (purple), iron (hot pink).

***Stylatula* sp.**

Figures 11A–B, 12A–B, 13A–F.

From the element linescan graph Figure 12B one can easily identify the dramatic drop of the calcium (in dark blue) weight percentage right on the range of the central core region, while other elements like carbon (in red), magnesium (in green), aluminum (in light green) and fluorine (in yellow) are increasing in value instead. Also noticeable are the void zones on both sides of the central core, which may probably be caused by the discontinuity of the surface on the boundaries between the core and the peripheral axis that ultimately resulted in the discontinuity of the X-ray detection as well. One single peak of calcium is shown in the central core region, which might be attributed to the broken pieces of debris from the more calcareous fringe of the core-axis intersection. The line patterns of most other elements like sodium (in dark green), silicon (in light blue), sulfur (in blue), strontium (in pink), ytterbium (in purple) and iron (in magenta) are relatively smooth compared to the big shifts of the line patterns of the elements mentioned above; thus, we know that those elements have more even overall distributions along the transect line.

Two area scans were performed between the two highly different atomic number contrast areas — the outer region of the axis and the central core — to determine the chemical compositions of the two distinct sites. From EDS results and the bar chart of spectrum 1, eleven elements were found as follows — three major elements: carbon (18.76 wt%), oxygen (40.09 wt%) and calcium (37.07 wt%); two minor elements: fluorine (1.47 wt%) and magnesium (1.48 wt%); and six trace elements: sodium (0.35 wt%), aluminum (0.08 wt%), iron (0.04 wt%), strontium (0.09 wt%) and REE ytterbium (0.22 wt%). The weight percentage of all elements can be seen in Table 6. This finding suggests that the outer region of the axis has a similar chemical distribution to most other species examined previously in having similar identified elements.

TABLE 6. EDS results of spectrum 1 for sea pen *Stylatula* sp. axial cross-section surface from Figure 13A. (All results are in weight%)

Element	C	O	F	Na	Mg	Al	S	Ca	Fe	Sr	Yb	Total
Spectrum 1 (Weight%)	18.76	40.09	1.47	0.35	11.48	0.08	0.35	37.07	0.04	0.1	0.22	100

Surprisingly, the EDS results from spectrum 2 showed dramatic changes in chemical composition of the central core; the most obvious change is the enormous drop in calcium weight percentage from 37.07 wt% to 0.32 wt%, making carbon a trace element, instead of as the always prominent major element; a large decrease in oxygen weight percentage is also observed, from 40.09 wt% to 8.46 wt%; while sulfur and iron weight percentage remain almost unchanged. Other changes include the addition of silicon and largely elevated amounts of carbon (from 18.76 wt% to 60.07 wt%), fluorine (from the previously 1.47 wt% to 24.14 wt%), and aluminum (from 0.08 wt% to 5.57 wt%), which make fluorine now a major element and aluminum now a minor element. The new discovery of barium is also surprising inasmuch as no other species examined here has been shown to contain barium. The overall element list for the identified twelve elements of spectrum 2 is shown in Table 7.

TABLE 7. EDS results of spectrum 2 for sea pen *Stylatula* sp. axial cross-section surface from Figure 13A. (All results are in weight%)

Element	C	O	F	Na	Mg	Al	Si	P	S	Ca	Fe	Ba	Total
Spectrum 2 (Weight%)	60.07	8.46	24.14	0.02	0.08	5.57	0.25	0.04	0.32	0.32	0.09	0.64	100



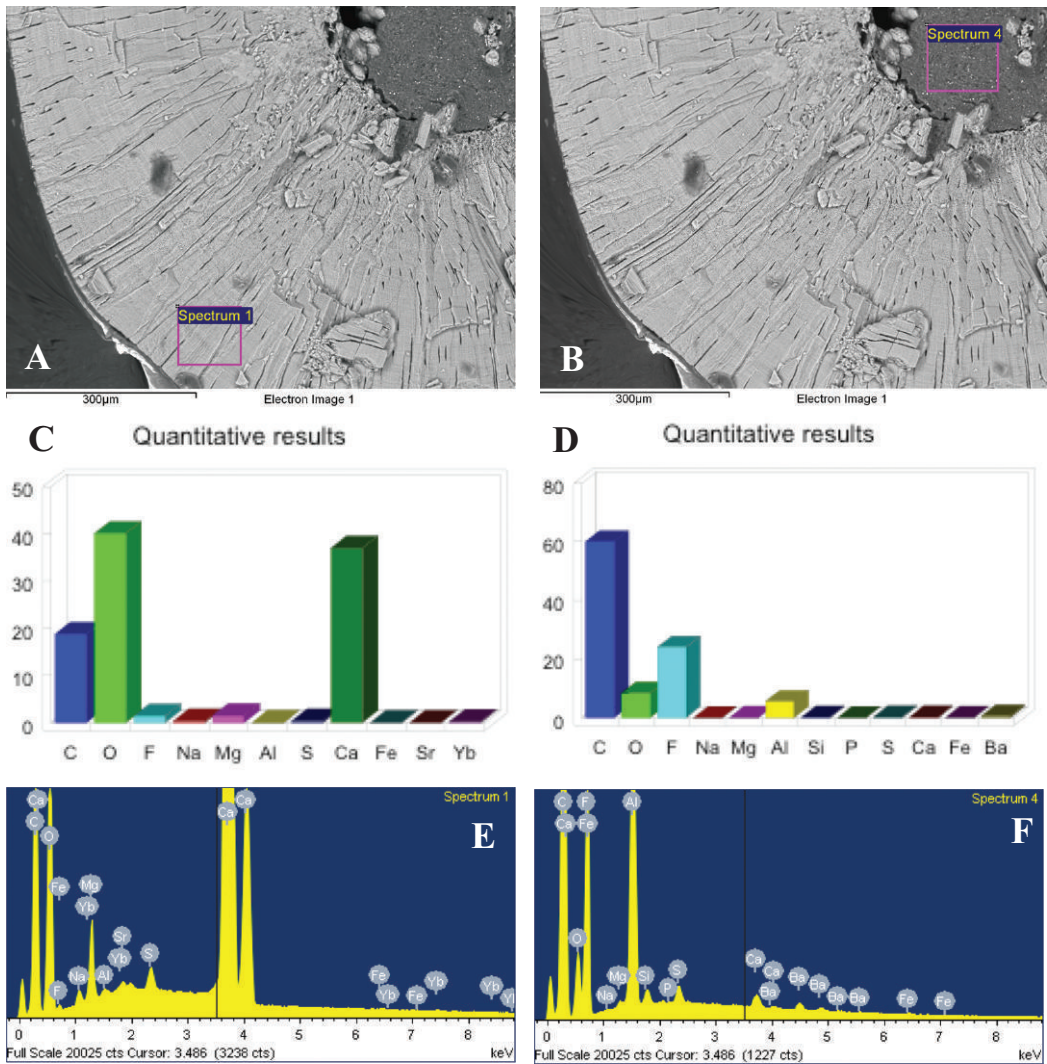


FIGURE 13. Energy dispersive spectrometer (EDS) area scan dataset. (A) and (B) EDS site of interest BSE image in a higher magnification cross-sectional view of the sea pen *Stylatula* sp. axial skeleton, acquired by INCA Energy software, partial area scans (spectrum 1 and 4) were applied for between site comparison purpose. Scale bar = 300  $\mu$ m. (C) and (D) Bar charts of the quantitative results from spectrum 1 and spectrum 4. (E) and (F) EDS results for spectrum 1 and 4.

### Among Taxa Comparison

The between-taxa comparison was made by selecting the shared elements by all species to be compared (Table 8), therefore trace elements like aluminum, silicon, phosphorous, chlorine, iron and bromine are not considered for comparison in this regard. Figure 14A shows the between-taxa elemental weight percentage comparison for the three gorgonians from three different families examined in this study: *Isis hippuris* (family Isididae), *Ellisella* sp. (family Ellisellidae) and *Plumigorgia hydroides* (family Plumigorgia). The trends of the three lines representing the three species are fairly similar and overlapping toward the end of chart where lies the higher atomic number elements; though some differences can be seen at the weight percentage value of carbon, oxygen, fluorine and magnesium.

TABLE 8. Summary of element distributions across taxa.

Elements shared by both gorgonians and sea pens:	C, O, F, Na, Mg, S, Ca, Yb
Elements shared by the three gorgonians:	C, O, F, Na, Mg, S, Ca, Sr, Yb
Elements shared by the four sea pens:	C, O, F, Na, Mg, S, Ca, Yb

Figure 14B shows the between-taxa elemental weight percentage comparison for the three sea pens from two different families examined in this study: *Cavernularia* sp. (family Veretillidae), *Virgularia* sp. (family Virgulariidae) and *Stylatula* sp. (family Virgulariidae). The trends of the lines representing *Cavernularia* sp. and *Virgularia* sp. are almost identical and differ only at the weight percentage value of the three major elements carbon, oxygen, and calcium. However, the line pattern of *Stylatula* sp. is significantly different from the two other species on all points of elements being compared, which is no doubt attributable to the bizarre chemical composition of the central core inside the axial skeleton.

The line chart presented in Figure 15 shows the great similarities on the elemental weight percentage comparison of eight common elements among the three gorgonians: *Isis hippuris* (family Isididae), *Ellisella* sp. (family Ellisellidae) and *Plumigorgia hydroides* (family Plumigorgia) and two sea pens: *Cavernularia* sp. (family Veretillidae), *Virgularia* sp. (family Virgulariidae). Although the weight percentage difference are visible at some points, it is still considered as having identical trends across taxa, except *Stylatula* sp. (family Virgulariidae), which has a very different line pattern due to the peculiar chemical composition of its central axis core.

### DISCUSSION

All EDS (Energy-dispersive X-ray spectroscopy) data shown here served as qualitative analyses only inasmuch as we were unable to achieve optimum quantitative accuracy inasmuch as the sample surfaces were unpolished (Oxford Instruments Plc. 2005). And, because of the unpolished samples, all EDS results were normalized by selecting the “All elements” processing option in “Quantitative Analysis Setup” section of the INCA software to force the analytical total to 100%. In addition, the carbon weight percent value is hard to define since the samples are all carbon coated. The reason to coat the samples with carbon is to prevent the M-family peaks of the metal-coating materials like platinum ( $M\alpha = 2.0485$ ), iridium ( $M\alpha = 1.9779$ ) and gold/palladium alloy ( $Au\ M\alpha = 2.1205$ ,  $Pd\ M\alpha = 2.8387$ ) from obscuring the identification and the analytical total of the K-family peaks of elements of interest, which may be present in the axial skeleton of the octocorals — such as silicon ( $K\alpha = 1.7398$ ), phosphorus ( $K\alpha = 2.0134$ ) and sulfur ( $K\alpha = 2.3075$ ).

All six specimens examined herein had the presence of ytterbium, the rare earth element (REE); according to research conducted by Sholkovitz and Shen (1995), Fallon et al. (2002), Wyn-

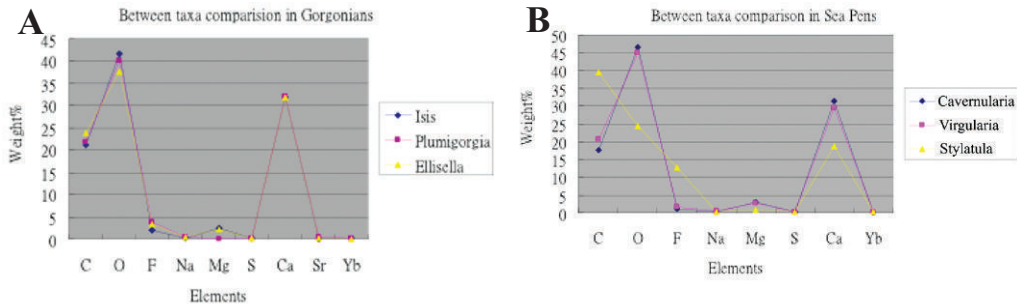


FIGURE 14. Line chart of the between-taxa elemental weight percentage comparison. (A) Between taxa comparison with the three gorgonians studied herein (*Isis hippuris*, *Plumigorgia hydroides* and *Ellisella* sp.). (B) Between taxa comparison within the sea pens studied herein (*Cavernularia* sp., *Virgularia* sp., and *Stylatula* sp.).

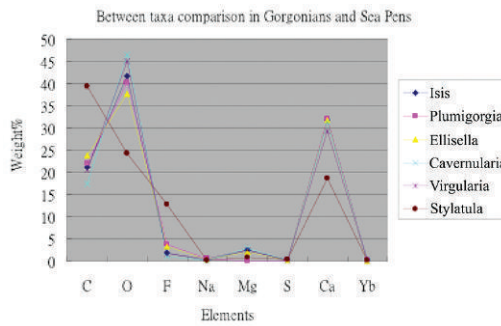


FIGURE 15. Line chart of the between-taxa elemental weight percentage comparison of both gorgonians and sea pens

dham et al. (2004) and Jupiter (2008), it is not rare to find REEs in coral skeleton lattices inasmuch as corals incorporate the REEs into the lattice by ionic substitution. The source of REEs and metals may come from the land via runoff events (Fallon et al. 2002), which may explain why various metals such as aluminum and iron can be found in some of the specimens, such as the *Stylatula* sp. collected right from the San Francisco Bay between Angel Island and Treasure Island, where there may be high degrees of impact due to the heavy populated locality.

The chemical composition across taxa between gorgonians and sea pens are for the most part similar and differ mostly by the trace elements that are present. As a result, the attempt to discern phylogenetic relationships depending on comparisons of chemical composition of axes among taxa is not sufficiently informative. However, it might seem promising to utilize the high-calcium content octocorals, such as the calcaxonian gorgonians and sea pens studied here, for environmental impact assessments in events like the *Deepwater Horizon* oil spill where impacts on deep-water octocorals were studied (White et al. 2012) or other anthropogenic influences such as mining and its impact on hard corals (Fallon et al. 2002). Both hard corals and octocorals as overall groups share similar extensive geographic and bathymetric ranges. Further investigation could compare the capability of recording ambient seawater elements in the skeletons of scleractinians with those in the axes of gorgonians and sea pens, preferably from the same transect site, to test the potential of using calcaxonian gorgonians and pennatulaceans for environmental impact studies.

Other than carbon, oxygen, and calcium, magnesium often shows a greater amount in some samples compared to the other minor elements. Folk (1974:45) states that sea water contains abundant magnesium ions and that any calcite cement that forms is rich in magnesium. An example would be cementing material that aids in the consolidation of octocoral axes.

## ACKNOWLEDGEMENTS

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**Additional Notes on North American Acanthaceae:  
Biogeography, Distributions, Taxonomy, Lectotypifications,  
and Catalog of Species**

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**A floristic and biogeographic summary of the Acanthaceae in the continental United States and Canada reveals 13 native genera containing 60 native species (with 19 endemic to the United States). A catalog of native and naturalized species that lists states/provinces of occurrence for each is provided. The distribution of *Dyschoriste oblongifolia* is confirmed in Louisiana, but excluded from Tennessee, Texas, and Virginia, in spite of previous attributions of the species to those states. The presence of *D. decumbens* is documented from southwestern New Mexico. An atypical form of *Justicia americana* with diffuse inflorescences from eastern Texas and Louisiana is discussed. Potentially naturalized, though undocumented as such, occurrences of *Pseuderanthemum variable*, an increasingly common greenhouse weed, are recorded out-of-doors in Florida and Louisiana. Typifications are discussed for eight names associated with species of North American Acanthaceae, and lectotypes are designated for five of them: *Dicliptera mollis*, *D. moritziana* var. *hirsuta*, *Hypoestes phyllostachya*, *Ruellia lacustris*, and *R. oblongifolia*.**

**KEYWORDS:** *Dyschoriste decumbens*, *D. oblongifolia*, *Justicia americana*, *Pseuderanthemum variable*, floristics, endemics, naturalized species.

During preparation of a forthcoming treatment of Acanthaceae for the *Flora of North America*, studies of collections from numerous herbaria in the United States and Europe have helped to resolve several taxonomic, distributional, and typification questions among North American taxa of the family. Discussions of and resolutions to some of these were provided by Daniel (2013); others are presented below.

**FLORISTIC AND BIOGEOGRAPHIC SUMMARIES OF ACANTHACEAE  
IN THE UNITED STATES AND CANADA**

Acanthaceae are represented in the continental United States and Canada (the region encompassed by the *Flora of North America*) by 19 genera (13 native) and 77 species (60 native). All of these species occur in the United States and one of them, *Justicia americana* (L.) Vahl, also occurs in southeastern Canada. A catalog of native and naturalized species in the continental United States and Canada, with their states or provinces of occurrence, is provided in Appendix I. Although no genera are restricted to this region of North America, 19 species (noted in Appendix I) are endemic to the United States, and at least seven additional species (*Dicliptera brachiata* (Pursh) Spreng., *Dyschoriste angusta* (A. Gray) Small, *Dyschoriste linearis* (Torr. & A. Gray) Kuntze, *Justicia americana* Vahl, *J. warnockii* B.L. Turner, *Ruellia metzae* Tharp, and *Stenandrium barbatum* Torr. & A. Gray) are nearly endemic there.

Figure 1 shows a map of the United States with the numbers of native species of Acanthaceae for each state, Canadian province, and federal district that have any. The largest genera in the United States and Canada are *Justicia* L. (14 native species, five of them endemic) and *Ruellia* L. (13 native species, 10 of them endemic). Among the states and provinces of the *Flora of North America* (FNA) project region, Texas (42 native species, including one endemic to the state) and Florida (22 species, including three endemic to the state) are the richest for Acanthaceae. Indeed, the highest numbers of taxa occur in the southern tier of states with species richness gradually decreasing by state in a northward direction, and with only a single species reaching southern Canada. This pattern is even more pronounced in the western United States where species are found only in the southern, arid portions of California, Arizona, and New Mexico. This pattern appears to reflect the generally tropical nature of the family. For comparison, there are about 400 species in Mexico, which occupies a considerably smaller landmass to the immediate south. Florida has the highest number of naturalized non-native species (17). Because of that state's subtropical climate, it is likely that additional non-natives that are cultivated or that become inadvertently introduced there will continue to become naturalized.

Based on their distributions, and to some extent on phylogenetic relationships, the Acanthaceae of the United States and Canada can be divided into three somewhat discrete geographic subregions with almost equal numbers of taxa: species of the southwestern United States (i.e., trans-Pecos Texas to southern California; see Daniel 1984, 2013, in press), species of Texas (excluding trans-Pecos counties; see Wasshausen 1966; Correll and Johnston 1970; Turner et al. 2003; Daniel 2011, in press), and species of the eastern and central United States (excluding Texas) and Canada (see Wasshausen 1998; Daniel in press). Each of these subregions is discussed below. Appendix II provides a species list for each subregion.

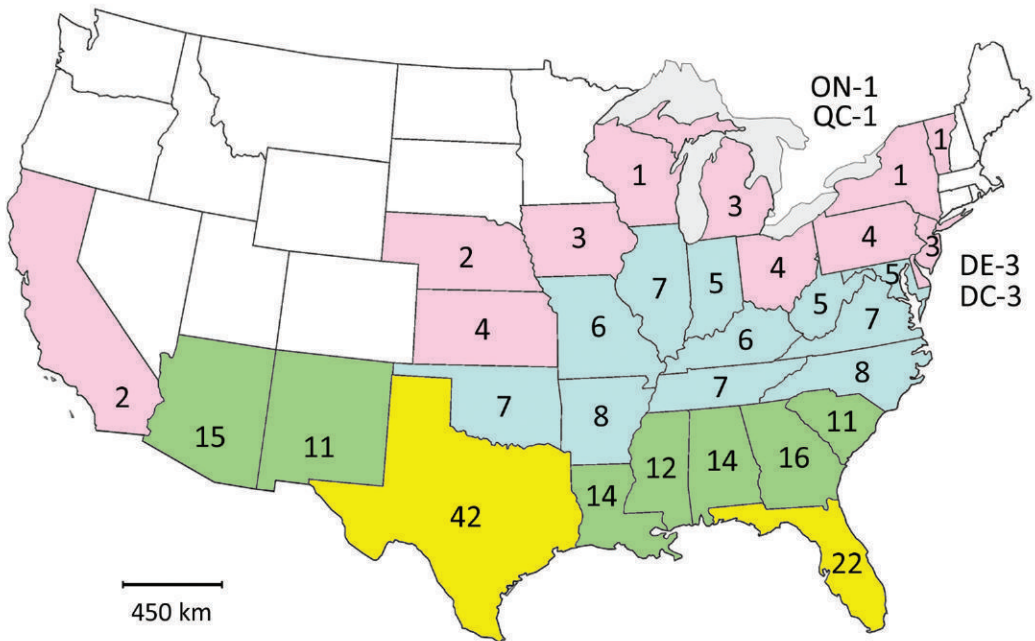


FIGURE 1. Map of the United States showing numbers of native species of Acanthaceae, if any, in each state, province of Canada, and federal district. Colors refer to states with 1–4 species (pink), 5–9 species (blue), 10–19 species (green), and 20 or more species (yellow). DC = District of Columbia, DE = Delaware, ON = Ontario (Canada), and QC = Québec (Canada).



**SOUTHWESTERN UNITED STATES SUBREGION.**—Species of this arid to semiarid subregion occur in desertscrub, desert grassland, and other biotic communities associated with the Chihuahuan and Sonoran deserts. Almost all of the 28 species of native Acanthaceae that occur here have more extensive ranges in desert and dry forest regions of western and central Mexico, and their occurrences in the southwestern United States represent the northern limit of their overall distributions. Floristically, this subregion shares the fewest taxa with the other subregions. Nineteen species of Acanthaceae from the FNA region are restricted to this subregion — the most for any of the subregions. The remaining nine species are all shared with the Texas (excluding trans-Pecos counties) subregion. Only one species, *Justicia americana*, is shared with both of the other subregions; however, its occurrence in the southwestern subregion is based on a single collection from the easternmost portion of the subregion, trans-Pecos Texas. Two genera, *Henrya* Nees and *Tetramerium* Nees, each represented by a single species here, have additional species to the south of the United States, but are not represented in the other subregions.

With seven species, *Carlowrightia* A. Gray, a genus of arid and semiarid regions, is the largest genus of Acanthaceae in the subregion. No species are endemic to this subregion, but *Justicia wrightii* A. Gray, is nearly so (also occurring in one county outside of, but bordering, the subregion). It occurs in Chihuahuan desertscrub and associated semiarid scrubland in western Texas and New Mexico, and its relatives appear to be morphologically similar species of the Chihuahuan Desert in Mexico and Texas (Daniel 2011). Molecular phylogenetic studies reveal that although *J. longii* Hilsenb. and *J. candicans* (Nees) L.D. Benson appear to be closely related, other species of *Justicia* occurring in this region (e.g., *J. sonorae* Wash. and *J. californica* (Benth.) D.N. Gibson) are not closely related to them or to each other (C. Kiel, personal communication). Daniel (1984) discussed the larger number of species of Acanthaceae in the southwestern United States that is associated with the Chihuahuan Desert than the Sonoran Desert. Factors limiting the spread of Acanthaceae in this subregion include: the Mediterranean climate to the west in California; a shift to colder desert and coniferous forest regions in northern California, Arizona, and New Mexico; and vegetational changes associated with the Edwards Plateau to the east in Texas.

**EASTERN AND CENTRAL UNITED STATES (EXCLUDING TEXAS) AND CANADA SUBREGION.**—Although it comprises the largest land mass by far in the FNA region, this subregion has 26 species of native Acanthaceae. This is about the same number of natives as occur in the southwestern United States; however, climate, species composition, and endemism differ substantially between the two subregions. Climate in the eastern and central United States varies from humid subtropical to humid continental, with significantly higher rainfall than the American Southwest. *Ruellia* (nine native species) and *Justicia* (six native species) are the largest genera of Acanthaceae in this subregion, and they include four and three species, respectively, that are endemic to it. Floristically, the subregion shares 13 species in common with the Texas (excluding trans-Pecos counties) subregion and one with the southwestern United States subregion. Twelve species of Acanthaceae from the FNA region occur only in this subregion. Ten of them, all restricted to the southeastern United States (from Maryland and West Virginia southward to Florida and westward to Louisiana), are endemic there. This is by far the largest number of endemics among the three subregions.

Known molecular phylogenetic relationships of plants occurring in this region show geographic structure. The three species of *Dyschoriste* Nees in the southeastern United States (*D. angusta*, *D. humistrata* (Michx.) Kuntze, and *D. oblongifolia* (Michx.) Kuntze) appear to form a clade along with a West Indian species (Chumchim et al., in press). Tripp (2007) demonstrated that several species of the eastern and central United States and the Texas (excluding trans-Pecos counties) subregions form a clade distinct from a clade containing other species from Texas and states to the west (however, two different accessions of *R. drummondiana* (Nees) A. Gray appeared, respective-

ly, in each of these clades). At least three of the five species of *Justicia* (*J. americana*, *J. lanceolata* (Chapm.) Small, and *J. ovata* (Walter) Lindau) that comprise a morphologically similar group of aquatic to subaquatic taxa (Daniel 2013) in both this and the Texas (excluding trans-Pecos counties) subregions form a well-supported clade (Carrie Kiel, personal communication).

Factors limiting the northward spread of most species of Acanthaceae in this subregion likely include cold winter temperatures. However, several species in this subregion have distributions extending farther northward than is typical for the family. The distribution of *Justicia americana*, the most geographically widespread species of the genus in the United States, extends farther northward (to ca. lat. 47°N in southeastern Canada) than any other species in the family. Based on their occurrences in the northern tier of states in the United States it appears that this and several other species (e.g., *Ruellia humilis* Nutt., *R. strepens* L.) occurring in, but not restricted to, this subregion have adapted to the cold winters of a temperate continental climate, at least to a certain degree.

**TEXAS (EXCLUDING TRANS-PECOS COUNTIES).**—Geographically, this subregion is positioned between and partly surrounded by the other two subregions. It is enriched by species from each, but is treated as distinct because it contains eight species that do not occur in them, and one endemic species, *Ruellia drummondiana* (Nees) A. Gray. It shares two genera, *Carlowrightia* A. Gray and *Anisacanthus* Nees, with the southwestern United States subregion that are absent from the eastern and central United States subregion, whereas it shares two other genera, *Avicennia* L. and *Yeatesia* Small, with the eastern and central United States subregion that are absent from the southwestern United States subregion. Twenty-nine species of Acanthaceae are native to the subregion. As is evident from the maps of Turner et al. (2003), the 13 species in common with the eastern and central United States (excluding Texas) and Canada subregion are more prominent in eastern and central Texas, whereas the nine species shared with the southwestern United States subregion (especially with those in the trans-Pecos counties of Texas) are more prominent in western and southwestern Texas. As in the southwestern United States subregion, this subregion is enriched by plants from the semiarid biotic communities (e.g., Tamaulipan thornscrub) in adjacent Mexico. Indeed, all of the plants noted above that only occur in this subregion (except the endemic *R. drummondiana*) within the United States are so derived.

Because of its geographic position and floristic composition, known phylogenetic affinities of species in this subregion are primarily with those of either of the two other subregions. For example, species of *Dyschoriste* in Texas (and adjacent Oklahoma; i.e., *D. crenulata*, *D. linearis*) and those from the southwestern United States appear to form a clade distinct from that of the three species in the southeastern United States (Chumchim et al., in press). The affinities of *J. americana* and *J. lanceolata* with plants otherwise known only from the eastern and central United States (as noted above) contrasts with the close affinities of *J. pilosella* to *J. candicans* and *J. longii* of the southwestern United States subregion (Carrie Kiel, personal communication).

Factors limiting the northward distributions of most species restricted to this subregion in the United States would appear to be low winter temperatures because, as noted above, they all appear to represent the northern extent of their respective species ranges. *Ruellia drummondiana*, which is endemic to this subregion, appears to be largely or completely confined to the calcareous Edwards Plateau. Its restricted distribution suggests adaptation to local (edaphic) conditions.

DOCUMENTED OCCURRENCES OF *DYSCHORISTE DECUMBENS* IN NEW MEXICO*Dyschoriste decumbens* (A. Gray) Kuntze

UNITED STATES. New Mexico. **Hidalgo Co.:** Gray Ranch in Animas Mountains, T31S, R18W, 6000 ft, 15 September 1990, *R. Dewitt Ivey 101* (UNM), 192 (UNM), 262 (UNM); along lower Indian Creek, N end of Animas Mountains, 5400 ft, 23 Jul 1975, *W. Wagner 1292* (UNM).

Kobuski (1928) recorded and mapped the occurrence of *Dyschoriste decumbens* in New Mexico based on collections of Charles Wright (1462, 1463; both at MO) from the “Valley of the Rio Grande” made in 1851. According to Johnston (1940) and Shaw (1987), at least *Wright 1463* was collected in western Texas (Pecos Co.: Escondido Springs to Comanche Springs [= Ft. Stockton]), and is probably referable to *D. cinerascens* (Henr. & Hilsenb.) T.F. Daniel (Daniel 2013). The locality of *Wright 1462* remains uncertain, but if collected from the Rio Grande Valley of New Mexico, it would also likely pertain to *D. cinerascens*. Martin and Hutchins (1981: Map 1052) noted the presence of *Dyschoriste decumbens* in Eddy County, New Mexico, and Daniel (1984) cited collections from Chaves, Eddy, and Lincoln counties in southeastern and south-central New Mexico. All collections of *Dyschoriste* from those counties were subsequently treated by Daniel (2013) as *D. cinerascens*. Daniel (2013) recently noted that *D. decumbens* is widespread in southeastern Arizona and northwestern Mexico, and uncommon in western Texas; its presence in southwestern New Mexico was shown on a map. The collections noted above from Hidalgo County document its occurrence in that county and state.

DISTRIBUTION OF *DYSCHORISTE OBLONGIFOLIA**Dyschoriste oblongifolia* (Michx.) Kuntze

UNITED STATES. Louisiana. **Natchitoches Parish:** Briarwood, near LA 9 and Readhimer [ca. 32°6.92'N, 92°59.195'W], 6 VI 1969, *R. Thomas et al. 13851* (NLU).

Of the three species of *Dyschoriste* Nees that occur in the southeastern United States, *D. oblongifolia* has the most extensive distribution and bears the largest flowers. Wasshausen (1998) noted the occurrence of this species in Alabama, Florida, Georgia, South Carolina, and Louisiana. Numerous collections from the former four states that conform to *D. oblongifolia* confirm its presence in each. Occurrence of the species in Louisiana has remained undocumented. Reports or collections from Virginia, Tennessee, and Texas also have been attributed to this species.

Various authors (e.g., Riddell 1852; Long 1970; MacRoberts 1989; Wasshausen 1998) noted the occurrence of this species in Louisiana; however, no documented occurrences were cited or seen. Featherman (1871) noted an occurrence of the species (as *Dipteracanthus oblongifolius* (Michx.) Chapm.) from “Farmersville” [= Farmerville] in Union Parish; this was undoubtedly the basis for MacRoberts’ (1989) map, which attributed the species to that parish. The species was not listed for the state by Thomas and Allen (1982), and was subsequently specifically excluded by them (Thomas and Allen 1996). Irrespective of whether the nineteenth century report of the species from Louisiana is based on an extant collection that has yet to be located or studied, the relatively recent collection noted above conforms to *D. oblongifolia* and confirms its presence in that state.

*Dyschoriste oblongifolia* has been noted to occur in Virginia on numerous occasions. Small (1903; as *Calophanes oblongifolia* (Michx.) D. Don) indicated that the species occurred from Virginia to Florida. In a monograph of the genus, Kobuski (1928:56) cited *Thurber s.n.* (GH) as “probably from [the] southeastern portion of the state.” Original data on this collection indicates “Southern States” and “Virginia,” but lacks both locality and date of collection. Fernald wrote on the specimen that its provenance was doubtful (cf. Fernald 1937: 477, 1945: 63). Fernald (1945) corrected

his identification of a collection (*Hunnewell 17361*) from Frederick County, Virginia from *D. oblongifolia* to *Ruellia humilis* Nutt. Gleason (1952) indicated that the species occurred in southeastern Virginia, but that it had not been observed there for many years. A specimen collected in 1841 (*Bailey s.n.*) at NY, at which herbarium both Small and Gleason worked, is attributed to Virginia. Because the specimen also lacks locality information, its provenance remains doubtful. Uttal (1983) noted that the species was long thought to occur in southeastern Virginia, but that no specimens from the state had come forth. The species was not treated in the recent *Flora of Virginia* (Weakley et al. 2012), and its occurrence (even historical) in that state remains both undocumented and doubtful.

A sterile collection from Tennessee (arid hills about Chattanooga, *G. Engelmann s.n.*, 25 Aug 1876, MO) was annotated by R. Hilsenbeck and A. Boyd as *D. oblongifolia*. Owing primarily to the lack of flowers and fruit, I was unable to associate this specimen with the species or the genus. While it is near the northern limit of the range of the species, it doubtfully pertains to *D. oblongifolia*.

*Durand 18* at PH from an undisclosed locale in Texas appears to represent *D. oblongifolia*, but because it lacks a specific locale and is out of the known range of the species, its occurrence in that state is treated as suspect and not recognized here. Numerous plants of *D. linearis* (Torr. & A. Gray) Kuntze from Texas have been erroneously identified as *D. oblongifolia*. *Dyschoriste linearis*, a species occurring from south-central Oklahoma to Mexico and common in central Texas (Daniel 2013), can appear superficially similar to *D. oblongifolia*. Both species have similarly shaped leaves (commonly oblanceolate to obovate) and relatively long corollas (18–31 mm). They can be distinguished on the basis of the ratio of the calyx lobes to the calyx tube, 2–3 in *D. linearis* and 3.1–5.8 in *D. oblongifolia*.

Thus, occurrences of *D. oblongifolia* have been documented from Alabama, Florida, Georgia, South Carolina, and Louisiana. The species likely also occurs in Mississippi; however, no collections of it from that state have been located.

#### AN UNUSUAL FORM OF *JUSTICIA AMERICANA* FROM LOUISIANA AND TEXAS

##### *Justicia americana* (L.) Vahl

UNITED STATES. Louisiana. **Lafourche Parish:** floating mat in Lake Boeff, *C. Sasser s.n.* (NLU). **St. Mary Parish:** island in Atchafalaya Bay, 28 Apr 1988 (flr), *F. Givens 5157* (LSU); Salt Point, S of rd. leading W to Picnic Area from LA 317 near its terminus at Burns, 29°34'14"N, 91°32'07"W, 22 May 2007 (flr), *C. Reid & P. Faulkner 6113* (LSU). **St. Tammany Parish:** Pearl River WMA, E side of West Pearl River just downstream from US 90 bridge, ca. 0.8 mi E of White Kitchen, 30 Sep 2003 (flr), *C. Reid & D. Moreland 4651* (LSU); Middle Pearl River N of US 90 and S of I-10 in Pearl River Wildlife Mgt. Area, *R. Thomas et al. 77143* (NLU); beside Mill Bayou at Middle Pearl River S of US 90, SE of Slidell, Sec. 6, T10S, R16E, *R. Thomas et al. 119696* (NLU). Texas. **Brazos Co.:** TAMU farm, 8 mi W of College Station, 30 Jun 1973 (flr), *J. Saichuk 65* (LSU). Madison Co.: Senator Ranch, Carr Lake, 23 May 1998, *A. Neill 1888* (TAMU).

All plants identified as *Justicia americana* from Louisiana (noted above), and some rare individuals so identified from eastern Texas (Daniel 2011; also noted above) grow in and along water bodies and have root systems (dense, fibrous, and extensive), foliage (mostly sessile to subsessile and linear to narrowly elliptic leaves), and corollas (e.g., lateral lobes of the lower lip diverging from the central lobe at angles of 45° or more) like typical representatives of the species (Fig. 2A). They differ from typical *J. americana*, which occurs from northern Mexico (Coahuila) to southern Canada (Ontario, Québec), by the opposite dichasia spread out along the inflorescence rachis to a

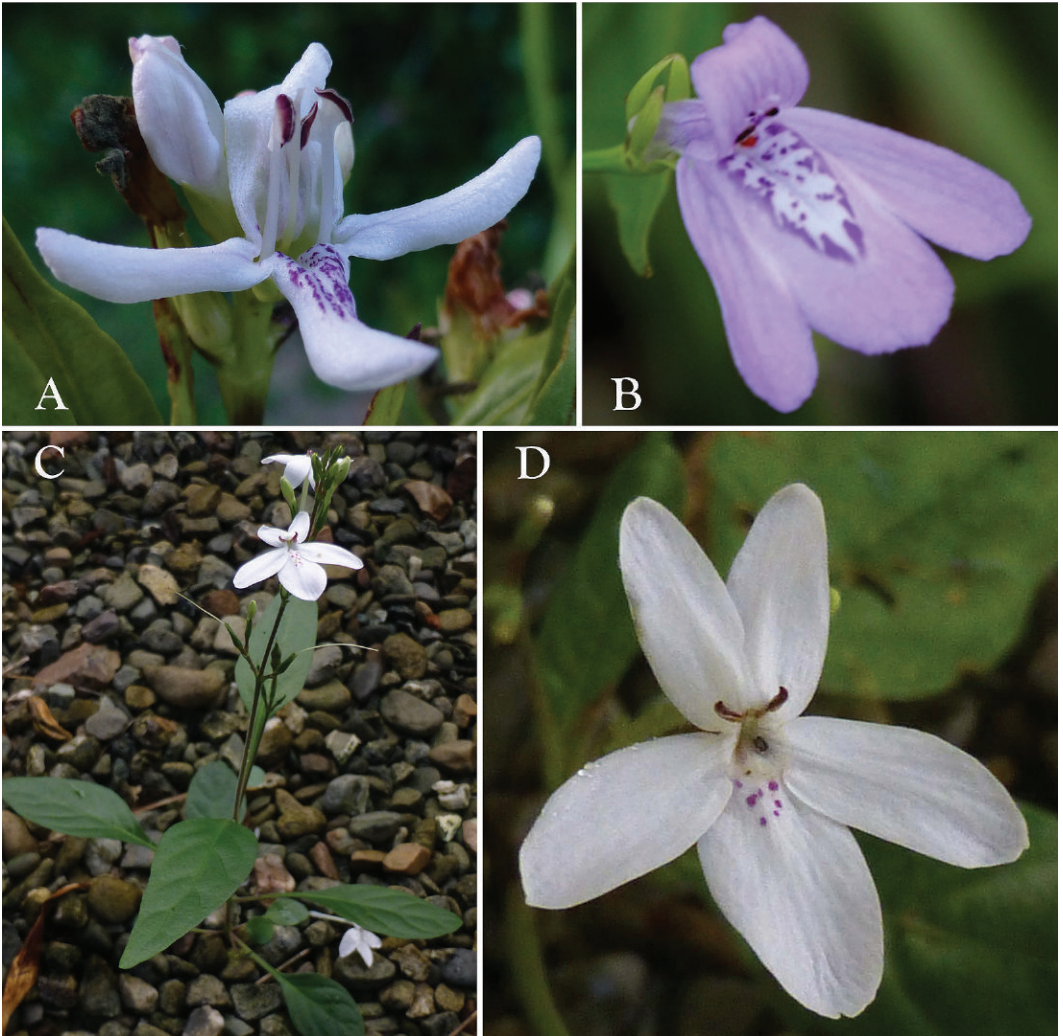


FIGURE 2. *Justicia* spp. (A, B) and *Pseuderanthemum variabile* (C, D). A. Flower of *J. americana* (Daniel & Lott 10530) showing limb of corolla with lateral lobes of lower lip widely spreading from lower-central lobe. B. Flower of *J. lanceolata* (Daniel 11762) showing limb of corolla with lateral lobes of lower lip barely spreading from lower-central lobe. There is variation in color of the corolla in both species of *Justicia*. C. Spontaneous plant of *P. variabile* at San Francisco Conservatory of Flowers (Daniel s.n.). D. Front view of limb of corolla.

greater extent. In typical representatives of the species, the spikes are headlike during anthesis with the median internodes mostly 1–3 mm long and the rachis is usually not or only partially visible. In the plants listed above, the spikes are more elongate with the median internodes 3.5–6 mm in length and the rachis is clearly visible. In this feature, they more closely resemble *J. ovata* in which the median internodes are 4 mm or more in length and the rachis is visible. The specimens listed above have been studied and can be characterized by the following description: perennial herbs growing in water, stout at base with a dense and extensive fibrous root system; leaves sessile to subsessile (petioles rarely up to 9 mm long on larger leaves), linear to narrowly elliptic, 32–125 × 7–24 mm, 4.1–7.1 × longer than wide; dichasia not headlike but ± elongate with median internodes of spike 3.5–6 mm long, rachis clearly evident. Similar root systems and leaves can be seen in other

southeastern species of *Justicia* (e.g., *J. lanceolata* when they grow in water, but corollas of *J. americana* (both typical plants and those with the more diffuse spikes) remain distinctive from both *J. lanceolata* (Fig. 2B) and *J. ovata* by their widely spreading lateral lobes of the lower lip.

Typical *Justicia americana* with the dense, headlike spikes is the common form of the species in Texas (primarily central Texas), but remains unknown from Louisiana. *Justicia lanceolata* is common in eastern Texas and throughout Louisiana, where it occurs in habitats similar to those of *J. americana*. The distributions of *J. americana* and *J. lanceolata* in Texas were mapped and discussed by Daniel (2011). The distribution of *J. ovata* is discussed below.

#### DISTRIBUTION OF *JUSTICIA OVATA*

*Justicia ovata* is known from Alabama, Florida, Georgia, North Carolina, South Carolina, and Virginia (e.g., Wasshausen 1998; Weakley 2012). It is especially well represented in the Atlantic coastal plain of the latter five states. Small (1903) had noted the distribution of this species from Virginia to Florida and Texas. The species has not been reported from Mississippi or Texas; however, two older collections at PH, purportedly from Louisiana (“N. Orleans,” without date or collector, and “Louisiana, Dr. Hale”), appear to represent the species, and might indicate a former or very rare occurrence in that state. Thomas and Allen (1982) listed only *J. lanceolata* from Louisiana. More recent references to *J. ovata* in Louisiana (e.g., MacRoberts 1989; Thomas and Allen 1996) pertain to plants of *J. lanceolata* (= *J. ovata* var. *lanceolata*) or the form of *J. americana* noted above, whereas others are ambiguous because collections are not cited (e.g., MacRoberts 1984). No recent collections of *J. ovata* from Louisiana have been located, and the current western extent of the range of this species appears to be in the Gulf coastal plain of the Florida panhandle and adjacent southern Alabama.

The species can usually be distinguished from *J. americana*, with which it is sometimes confused, by its less dense spikes and generally shorter and broader medial and distal leaves and less widely divergent lateral lobes of the lower lip of the corolla (which diverge from the lower-central lobe at angles less than 45°). Daniel (2011) discussed plants intermediate between *J. ovata* and *J. americana* in eastern North Carolina and southeastern Virginia, and between *J. ovata* and *J. lanceolata* in northern Florida. A specimen (*Grubbs 1013* at GA) from Hickman Co., Kentucky (in the Mississippi Embayment physiographic region of the westernmost corner of that state) appears to represent *J. ovata* based on apparently opposite dichasia above basal node of inflorescences. However, the inflorescences are incompletely formed on this specimen, and it is possibly an abnormal individual of *J. lanceolata* or a hybrid between that species and *J. americana* (which occurs in western Kentucky). The leaves are more like those of *J. lanceolata* (e.g., narrowly elliptic and 4.3–7.8 times longer than wide), which occurs in nearby regions of Missouri and Illinois, and in nearby counties of westernmost Kentucky).

#### SPONTANEOUS OCCURRENCES OF *PSEUDERANTHEMUM VARIABLE*

##### *Pseuderanthemum variable* (R. Br.) Radlk.

UNITED STATES. Florida. **Orange Co.:** NW side of Lake Wauseon, several plants spontaneous in highly mulched backyard, 13 Oct 1993 (flr), *N. Coile 7009* (US).

Louisiana. **East Baton Rouge Parish:** garden of house on Pastureview Drive, Baton Rouge, 22 Oct 2004 (flr, frt), *M. Standifer s.n.* (LSU).

This herbaceous species, which is native to New Guinea, New Caledonia, and tropical and temperate regions of Australia (Barker 1986), and which is apparently not cultivated in the United States, was noted to be an outdoor garden or yard weed on the collections noted above from

Louisiana and Florida. Previously it has been reported in the United States as a weed in and around greenhouses in Florida and South Carolina (Nelson and Kelly 1997). Indeed, it also occurs as a greenhouse weed in California (e.g., *Daniel s.n.*, CAS, from the Conservatory of Flowers in San Francisco; *Nisbet s.n.*, CAS, from private orchid greenhouse in Bolinas), Illinois (e.g., *Hill 34391*, NY, from a research greenhouse in Champaign County), Pennsylvania (*Armstrong s.n.*, CAS, from Morris Arboretum in Philadelphia; *Mounton s.n.*, US, from a greenhouse in western Pennsylvania), and New York (e.g., *Nee 58143*, NY, from the Nolen Greenhouses at the New York Botanical Garden). In most of these instances, it occurs as a weed in pots or on the ground in greenhouses, usually in those growing orchids. It is possible that seeds of *P. variable* have contaminated a commercial potting mix, bark, moss, or other growing media commonly used for orchids. Images (Fig. 2C, D) and a brief description of this species as it occurs as a spontaneous weed are provided below. *Coile 7009* notes that plants overwintered and reseeded in a year without freezing temperatures. Plants are undoubtedly self-compatible (like several other species of the genus; Daniel unpublished), and those occurring both in greenhouses and out-of-doors in the United States set fruit and appear to spread by seeds. Whether the species will persist as a naturalized occurrence out-of-doors or will be only a sporadic waif remains to be determined. It is not currently treated as a naturalized species in the account of Acanthaceae for the *Flora of North America* (Daniel, in press), but additional occurrences of it should be documented to help determine its status.

Erect and usually monocaulous herbs to 3 dm tall. Stem pubescent with flexuose to retrorse eglandular trichomes. Leaves petiolate, blades ovate to elliptic, 17–103 mm long, 5–32 mm wide, 2.2–3.4 × longer than wide, (rounded to) acute at apex, cuneate to attenuate at base. Inflorescences of axillary pedunculate dichasia to 65 mm long (including peduncle and excluding corollas) and terminal pedunculate dichasiate spikes to 165 mm long (including peduncle and excluding corollas), axillary and terminal peduncles pubescent with glandular and eglandular trichomes, axillary dichasia mostly 3-many-flowered, dichasia of terminal spikes 1–3-flowered. Bracts and bracteoles subulate, 1–2.5 mm long. Flowers pedicellate. Calyx 3–4.5 mm long, lobes subulate to lance-subulate. Corolla subsalverform, white to pale pink or lilac with maroon or purplish spots at base of lower-central lobe of corolla, (19-) 24–27 mm long, externally pubescent with eglandular trichomes, tube subcylindric (narrowed distally), longer than limb. Capsule 11–13 mm long, externally pubescent with erect to retrorse eglandular trichomes.

Another herbaceous *Pseuderanthemum*, *P. alatum* (Nees) M.R. Almeida. (including a bronze-leaved form known as chocolate plant), native to Mexico and Central America, is commonly cultivated in North American greenhouses as a ground cover or oddity. Sometimes it is also cultivated as a warm season annual in pots or ground plantings out-of-doors (e.g., in Louisiana, *Buras 316* at LSU), and might be expected to become naturalized by the spread of seeds in frost-free regions of the United States. It differs from *P. variable* by its distinctive proximal leaves (cordate to truncate to rounded and then long decurrent at base); shorter calyx (1.5–3 mm long); and longer (32–45 mm long), externally glabrous, and rose-pink corollas.

#### LECTOTYPIFICATIONS AND NOTES ON TYPES

The following lectotypifications and notes on types pertain to names associated with Acanthaceae of the FNA region.

1. *Dicliptera glandulosa* Scheele, Linnaea 21:765. 1848. *Dicliptera brachiata* var. *glandulosa* (Scheele) Fernald, Rhodora 43:287. 1941. TYPE. U.S.A. **Texas**: Comal Co., shady forest along river at New Braunfels, Oct, *Lindheimer s.n.* (fide protologue; no specimens located).

The location of Scheele's types is unknown (Stafleu and Cowan 1985). At BM and GH (and

likely in other herbaria, as well) there are duplicates of a collection that represents either type material or material from the same general region (Texas: Comal Co., “Comanche Spring: New Braunsfels, etc.,” 1850, *Lindheimer 1062*). If type material that corresponds to the protologue cannot be located, a specimen of this collection would likely serve well as a neotype.

Current taxonomic status. Synonym of *Dicliptera brachiata* (Pursh) Spreng.

2. *Dicliptera mollis* Nees in Alph. de Candolle, Prodr. 11:490. 1847. TYPE. MEXICO. **Veracruz**: Zacuapan, Feb 1838, *J. Linden 1081* (lectotype, designated here: K ex Hook.!; isolectotypes: G!, MICH!).

In the protologue of this species Nees (1847) cited three collections, all mounted on the same sheet in Hooker’s herbarium at K. Among these, the lectotype possesses leaves and more closely corresponds to the protologue. The other syntypes consist of: Veracruz: cordillera, bois de Zacuapan, 3000 ft, Jun–Oct 1840, *H. Galeotti 930* (syntype: K ex Hook.!; isosyntypes: BR!, G!) and Oaxaca: cordillera, 5000–6000 ft., Nov–Apr 1840, *H. Galeotti 923* (syntype: K ex Hook.!).

Current taxonomic status. Synonym of *Dicliptera sexangularis* (L.) Juss.

3. *Dicliptera moritziana* S. Schauer ex Nees var. *hirsuta* Nees in Alph. de Candolle, Prodr. 11:479. 1847. TYPE. U.S.A. **Texas**: San Felipe (see below), 1835, *Drummond 254* (lectotype, designated here: K ex Benth.!; isolectotypes: K ex Hook.!, OXF!, W!).

In the protologue of this variety, Nees (1847) cited two collections (218 and 254) of Drummond from Texas in Bentham’s herbarium at Kew, both of which he annotated. *Drummond 218* at K bears neither locality nor date of collection. Although both syntypes agree equally well with the protologue, the lectotype has more fertile material and appears to be slightly more hirsute than *Drummond 218*. A duplicate of the lectotype in Hooker’s herbarium at K notes a locality, San Felipe. This specimen was neither annotated nor cited by Nees.

Current taxonomic status. Synonym of *Dicliptera brachiata* (Pursh) Spreng. Specimens of *Drummond 213* from Texas at K, OXF, and TCD also pertain to this species.

4. *Hypoestes phyllostachya* Baker, J. Linn. Soc., Bot. 22:511. 1887. TYPE. MADAGASCAR. “Central Madagascar,” *Baron 4907* (lectotype, designated here: K!; isolectotype: P!).

Two Malagasy collections were cited in the protologue (Baker 1887) without indication of a type. In the introduction to his paper Baker (1887) noted that a shipment of plants had been received from Rev. R. Baron in Madagascar, and that the new species were based on these. Because Baker worked at K, it seems prudent to assume that his original materials (i.e., collections of Baron) are there. The other collection cited by Baker was made by the German collector J.M. Hildebrandt; this specimen was likely received at K from B, where Hildebrandt worked. Both specimens bear the same two sets of handwriting: 1) a large scrawl with Baker’s name of the plant on *Baron 4907* and with “*Hypoestes near lasiostegia* Nees” on *Hildebrandt 3444*, and 2) a smaller and neater handwriting that provides the place of publication on both sheets and that provides Baker’s name on *Hildebrandt 3444* and the word “type” on *Baron 4907*. Because the larger handwriting matches that on other specimens at K annotated by Baker, the indication of “type” would not appear to have been made by him. Thus lectotypification becomes necessary for *H. phyllostachya*. Both specimens are ample and correspond to the protologue. Data for the other syntype consists of: “West Madagascar,” Trabonji, Waldschatten, May 1880, *Hildebrandt 3444* (syntype: K!; isosyntypes: CORD-image!, P!).

Current taxonomic status. *Hypoestes phyllstachya* Baker.

5. *Justicia ensiformis* (Walt.) Elliott, Sketch, 1: 11. 1816. *Dianthera ensiformis* Walt., Fl.



Carol. 63. 1788, non *Dianthera ensiformis* Wood (1870). TYPE. Not designated (no specimens, localities, or reference to other original materials were cited in the protologue). On making the combination in *Justicia*, Elliott (1816:11) noted that he had only seen specimens without flowers, and: “Grows in St. John’s, Dr. Macbride. Flowers May.” The latter information might conform to a specimen that would be an appropriate choice for a neotype.

Current taxonomic status. *Justicia americana*?

6. *Justicia linearifolia* Lam., Encycl. 1:632. 1785, nom. illegit. *Dianthera linearifolia* (Lam.) Raf., Autikon Bot. 29. 1840.

In the protologue of *J. linearifolia*, Lamarck (1785) cited *Dianthera americana* L. as a synonym. Thus Lamarck’s name is superfluous (and illegitimate) because he should have used Linnaeus’ epithet in a new combination.

Current taxonomic status. *Justicia americana* (L.) Vahl.

7. *Ruellia lacustris* Schlecht. & Cham., Linnaea 5:96. 1830. *Hygrophila lacustris* (Schltdl. & Cham.) Nees in A. de Candolle, Prodr. 11:86. 1847. TYPE. MEXICO. **Veracruz**: Laguna de Jalapa, Sep 1828, *Deppe & Schiede 123* (lectotype, designated here (or perhaps holotype): HAL!).

The specimen at HAL is designated as the lectotype because it appears to contain several field labels, is a complete specimen, and is the only specimen of the collection known to me. It is possible that there was a specimen at B (since destroyed), where Schlechtendal worked (before relocating to HAL; see Stafleu and Cowan 1985) when this species was collected and described, however I have found no record of such.

Current taxonomic status. Synonym of *Hygrophila costata* Nees.

8. *Ruellia oblongifolia* Michx., Fl. Bor.-Am. 2: 23. 1803. *Calophanes oblongifolia* (Michx.) D. Don in Sweet, Brit. Fl. Gard. 2: t. 181. 1833. *Dipteracanthus oblongifolius* (Michx.) Chapm., Fl. Southeastern U.S., 303. 1860. *Dyschoriste oblongifolia* (Michx.) Kuntze, Rev. Gen. Pl. 2: 486. 1891. TYPE. U. S. A. **Georgia**: “Georgie,” without date or collector (lectotype, designated here: P-Michx.! i.e., specimen shown in Michaux Herb. microfiche 79/16—fiche 79, image no. 16).

In the Michaux herbarium at P there are two specimens that pertain to this species and both of them bear flowers and fruits. One of these (Michaux Herb. microfiche 79/16—fiche 79, image no. 16) has a label stating “*Ruellia oblongifolia*, Georgie,” and was marked as a “type” at an unknown later time. The other specimen (Michaux Herb. microfiche 79/15) bears two labels, one of which states, “No. 14 *Ruellia*, Le 27 Avril, Ex am. la capsule,” and the other states, “*Ruellia biflora*, stigma simplex.” The specimen identified with both the name and locality that appear in the protologue is chosen as the lectotype.

Current taxonomic status: *Dyschoriste oblongifolia* (Michx.) Kuntze.

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## Appendices

### Appendix I

Catalog of native and naturalized species in Canada and the continental United States and their province(s), state(s), and federal district(s) of occurrence. Canadian provinces are spelled-out whereas standard US postal abbreviations are used for states and the District of Columbia in the United States. Occurrences are based on one or more specimens studied. A few additional occurrences that have been reported, but not confirmed during my studies, are noted with a question mark; they are not included in the numerical totals shown in Figure 1. Numbers in parentheses following generic names refer to the number of species recognized in the region of this study. <sup>E</sup> = endemic to the continental United States, \* = naturalized non-native.

#### *Anisacanthus* Nees (4)

- A. linearis* (S.H. Hagen) Henr. & E.J. Lott: TX
- A. puberulus* (Torr.) Henr. & E.J. Lott: TX
- A. quadrifidus* (Vahl) Nees: TX
- A. thurberi* (Torr.) A. Gray: AZ, NM

#### \**Asystasia* Blume (1)

- \**A. gangetica* (L.) T. Anderson: FL

#### *Avicennia* L. (2)

- A. germinans* (L.) L.: FL, LA, MS, TX
- \**A. marina* (Forssk.) Vierh.: CA

#### \**Barleria* L. (2)

- \**B. cristata* L.: FL
- \**B. lupulina* Lindl.: FL

#### *Carlowrightia* A. Gray (8)

- C. arizonica* A. Gray: AZ, CA, TX
- C. linearifolia* (Torr.) A. Gray: AZ, NM, TX
- C. mexicana* Henr. & T.F. Daniel: TX
- C. parviflora* (Buckley) Wassh.: TX
- C. parvifolia* Brandege: TX
- C. serpyllifolia* A. Gray: TX
- C. texana* Henr. & T.F. Daniel: AZ, NM, TX
- C. torreyana* Wassh.: TX

#### *Dicliptera* Juss. (3)

- D. brachiata* (Pursh) Spreng.: AK, AL, FL, GA, IL, IN, KS, KY, LA, MS, MO, NC, OK, SC, TN, TX, VA
- D. resupinata* (Vahl) Juss.: AZ
- D. sexangularis* (L.) Juss.: FL, TX

#### *Dyschoriste* Nees (7)

- D. angusta* (A. Gray) Small: FL,
- D. cinerascens* (Henr. & Hilsenb.) T.F. Daniel: NM, TX
- D. crenulata* Kobuski: TX
- D. decumbens* (A. Gray) Kuntze: AZ, NM, TX
- <sup>E</sup>*D. humistrata* (Michx.) Kuntze: FL, GA, SC
- D. linearis* (Torr. & A. Gray) Kuntze: OK, TX
- <sup>E</sup>*D. oblongifolia* (Michx.) Kuntze: AL, FL, GA, LA, SC

*Elytraria* Michx. (3)*E. bromoides* Oerst.: TX<sup>E</sup>*E. caroliniensis* (J.F. Gmel.) Pers.: FL, GA, SC*E. imbricata* (Vahl) Pers.: AZ, NM, TX*Henrya* Nees ex Benth. (1)*H. insularis* Nees ex Benth.: AZ*Hygrophila* R. Br. (3)<sup>\*</sup>*H. corymbosa* (Blume) Lindau: FL, TX*H. costata* Nees & T. Nees: AL, FL, GA, LA, MS, TX<sup>\*</sup>*H. polysperma* (Roxb.) T. Anderson: FL, SC, TX<sup>\*</sup>*Hypoestes* Sol. ex R. Br. (1)<sup>\*</sup>*H. phyllostachya* Baker: FL*Justicia* L. (17)*J. americana* (L.) Vahl: Ontario, Québec; AK, AL, DC, DE, FL, GA, IA, IL, IN, KS, KY, LA, MD, MI, MS, MO, NC, NJ, NY, OH, OK, PA, SC, TN, TX, VT, VA, WV<sup>E</sup>*J. angusta* (Chapm.) Small: FL<sup>\*</sup>*J. brandegeana* Wssh. & L.B. Sm.: FL, TX*J. californica* (Benth.) D.N. Gibson: AZ, CA*J. candidans* (Nees) L.D. Benson: AZ<sup>E</sup>*J. crassifolia* (Chapm.) Small: FL<sup>E</sup>*J. lanceolata* (Chapm.) Small: AK, AL, FL, GA, IL, KY, LA, MO, MS, OK, TN, TX*J. longii* Hilsenb.: AZ, TX<sup>E</sup>*J. ovata* (Walter) Lindau: AL, FL, GA, LA?, NC, SC, VA*J. pacifica* (Oerst.) Hemsl.: TX<sup>\*</sup>*J. pectoralis* Jacq.: FL*J. pilosella* (Nees) Hilsenb.: NM, TX*J. pringlei* B.L. Rob.: FL*J. sonorae* Wssh.: AZ<sup>\*</sup>*J. spicigera* Schldl.: FL*J. warnockii* B.L. Turner: TX<sup>E</sup>*J. wrightii* A. Gray: NM, TX<sup>\*</sup>*Nelsonia* R. Br. (1)<sup>\*</sup>*N. canescens* (Lam.) Spreng.: FL<sup>\*</sup>*Odontonema* Nees (1)<sup>\*</sup>*O. cuspidatum* (Nees) Kuntze: FL*Ruellia* L. (15)<sup>\*</sup>*R. blechum* L.: FL<sup>E</sup>*R. caroliniensis* (J.F. Gmel.) Steud.: AK, AL, DC, DE, FL, GA, IL, IN, KY, LA, MD, MS, NC, NJ, OH, OK?, PA, SC, TN, TX, VA, WV*R. ciliatiflora* Hook.: <sup>\*</sup>AL?, AZ, <sup>\*</sup>FL, <sup>\*</sup>GA, <sup>\*</sup>LA, <sup>\*</sup>MS, TX<sup>E</sup>*R. ciliosa* Pursh: AL, FL, GA, LA, MS, NC, SC<sup>E</sup>*R. drummondiana* (Nees) A. Gray: TX<sup>E</sup>*R. humilis* Nutt.: AK, AL, FL, GA, IA, IL, IN, KS, KY, LA, MD, MI, MO, MS, NE, NC, OH, OK, PA, TN, TX, VA, WV, WI*R. metzae* Tharp: TX<sup>E</sup>*R. noctiflora* (Nees) A. Gray: AL, FL, GA, LA, MS*R. parryi* A. Gray: AZ, NM, TX<sup>E</sup>*R. pedunculata* Torr. ex A. Gray: AK, AL?, IL, LA, MO, OK, TX<sup>E</sup>*R. pinetorum* Fernald: AL, FL, GA, LA, MS, SC, TX

<sup>E</sup>*R. purshiana* Fernald: AL, GA, MD, NC, SC, TN, VA, WV

\**R. simplex* Wright: AL, AZ, FL, GA, LA, MS, TX

<sup>E</sup>*R. strepens* L.: AK, AL, DC, DE, GA, IA, IL, IN, KS, KY, LA, MD, MI, MO, MS, NC, NE, NJ, OH, OK, PA, SC, TN, TX, VA, WV

<sup>E</sup>*R. succulenta* Small: FL

*Stenandrium* Nees (2)

*S. barbatum* Torr. & A. Gray: NM, TX

*S. dulce* (Cav.) Nees: FL, TX

*Tetramerium* Nees (1)

*T. nervosum* Nees: AZ, NM, TX

\**Thunbergia* Retz. (3)

\**T. alata* Bojer ex Sims: AL, AK, FL, GA, TX

\**T. fragrans* Roxb.: FL

\**T. grandiflora* Roxb.: FL, TX

*Yeatesia* (2)

*Y. platystegia* (Torr.) Hilsenb.: TX

<sup>E</sup>*Y. viridiflora* (Nees) Small: AK, AL, FL, GA, LA, MS, TX

## Appendix II

### Lists of native species of Acanthaceae in each subregion noted in the text.

SOUTHWESTERN UNITED STATES SUBREGION (28): *Anisacanthus linearis*, *A. puberulus*, *A. thurberi*; *Carlowrightia arizonica*, *C. linearifolia*, *C. mexicana*, *C. parvifolia*, *C. serpyllifolia*, *C. texana*, *C. torreyana*; *Dicliptera resupinata*; *Dyschoriste cinerascens*, *D. decumbens*, *D. linearis*; *Elytraria imbricata*; *Henrya insularis*; *Justicia americana*, *J. californica*, *J. candicans*, *J. longii*, *J. pilosella*, *J. sonora*, *J. warnockii*, *J. wrightii*; *Ruellia ciliatiflora*, *R. parryi*; *Stenandrium barbatum*; *Tetramerium nervosum*.

TEXAS (EXCLUDING TRANS-PECOS COUNTIES) SUBREGION (29): *Anisacanthus quadrifidus*; *Avicennia germinans*; *Carlowrightia parviflora*, *C. texana*, *C. torreyana*; *Dicliptera brachiata*, *D. sexangularis*; *Dyschoriste crenulata*, *D. linearis*; *Elytraria bromoides*; *Hygrophila costata*; *Justicia americana*, *J. lanceolata*, *J. pacifica*, *J. pilosella*, *J. warnockii*, *J. wrightii*; *Ruellia caroliniensis*, *R. ciliatiflora*, *R. drummondiana*, *R. humilis*, *R. metzae*, *R. parryi*, *R. pedunculata*, *R. pinetorum*, *R. strepens*, *Stenandrium dulce*; *Yeatesia platystegia*, *Y. viridiflora*.

EASTERN AND CENTRAL UNITED STATES (EXCLUDING TEXAS) AND CANADA SUBREGION (26): *Avicennia germinans*; *Dicliptera brachiata*, *D. sexangularis*; *Dyschoriste angusta*, *D. humistrata*, *D. linearis*, *D. oblongifolia*; *Elytraria caroliniensis*; *Hygrophila costata*; *Justicia americana*, *J. angusta*, *J. crassifolia*, *J. lanceolata*, *J. ovata*, *J. pringlei*; *Ruellia caroliniensis*, *R. ciliosa*, *R. humilis*, *R. noctiflora*, *R. pedunculata*, *R. pinetorum*, *R. purshiana*, *R. strepens*, *R. succulenta*; *Stenandrium dulce*; *Yeatesia viridiflora*.

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